OUT OF AFAR: THE FIRST HOMININ MIGRATION? LONG-TERM LANDSCAPE CHANGES IN THE AFAR REGION AND IMPLICATIONS FOR HOMININ BIPEDALISM.

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ABSTRACT

Tectonic and geomorphological processes in East Africa have long shaped the environments within which hominins evolved, with the Afar Depression and adjacent Main Ethiopian Rift, created through rifting and plate reorganisation, providing an important setting in which landscape isolation may have influenced evolutionary opportunity. Climate change in Africa has traditionally been regarded as the main driver of adaptations such as hominin bipedalism, often considered separately from the tectonic and geomorphic setting in which it arose. This study evaluates a refugial scenario for bipedalism that situates the evolution of hominin bipedalism within the tectonic and geomorphic history of the Afar region.

A GIS-assisted reconstruction of successive tectonic stages, basin development, and changing drainage patterns, integrating published geological syntheses, DEM-derived topographic context, and selected source-checked locality records, provides a spatial framework for evaluating isolation, faunal migration, and the opening of dispersal corridors. The reconstruction indicates that geological isolation may have altered faunal exchange and predation exposure, contributing to refugial conditions in which upright behaviours could emerge in concert with climate-driven pressures. By ca. 4.2 Ma, the Main Ethiopian Rift corridor, established by ca. 5 Ma, may have become sufficiently permeable to enable southward dispersal, coinciding with the earliest secure evidence for bipedal hominins in the Turkana record. Their emergence in the region, after earlier gaps in the fossil record, may reflect the first hominin migration ‘out of Afar’ and into wider Africa. By combining fossil distributions with GIS-assisted landscape history, this study argues that tectonic and topographic isolation may have been a major, underappreciated component of the context in which early bipedalism evolved, alongside climate-driven pressures.

1. INTRODUCTION

Tectonic and geomorphological processes have long shaped the environments and ecosystems of Africa, particularly since the Miocene, and have provided the backdrop against which hominins evolved [1-4]. Africa also contains a rich primate fossil record, including hominins stretching back as far as the Oligocene [5-8]. Within this broader context, the Afar Depression and the adjacent Main Ethiopian Rift form a tectonically active, geomorphologically complex region that is central to discussions of early hominin evolution and dispersal.

Interpretations based on first and last appearances must be treated cautiously because the fossil record is uneven in both space and time. Given uneven preservation, exposure, sampling intensity, and dating precision, we treat the fossil record as a set of constraints, not a complete census [9-11].

How bipedalism was acquired within the hominins, and the anatomical changes and locomotor patterns that facilitated these behaviours, has been a source of much debate [e.g., 12, 13-18]. However, despite the multiple locomotor hypotheses to explain the hominin behavioural adaptations, many propose that climatic cooling and drying trends were highly influential [e.g., 19, 20-22]. At its simplest, the climate hypothesis suggests that the progressive development of open grasslands favoured the adoption of bipedalism through three broad, not necessarily sequential phases: facultative, habitual, and obligate [e.g., 23]. We recognize that this three-stage framework, *Ardipithecus* as a facultative biped, *Australopithecus* as habitual, and later *Homo* as obligate, is a simplified outline of more complex locomotor behaviour, but it does capture a broadly accepted trend in the fossil record. Recent discoveries at Ledi–Geraru [24], where *Australopithecus* and early *Homo* co-existed in the Afar Region between about 2.78 and 2.59 Ma, underline that these locomotor modes could overlap in time and space and that Afar sustained multiple hominin lineages simultaneously, consistent with repeated occupation and persistence under changing conditions.

A central question is what kind of environment would favour the early stages of bipedalism (facultative) when adaptation itself would have been nascent, but the risk of predation would have been high. As habitual bipedality became more established, reliance on climbing for predator avoidance likely declined, even if climbing ability persisted, as predation risk was increasingly managed through terrestrial efficiency, vigilance, grouping behaviour, and access to protective terrain. Several alternative ideas have been advanced, including the postural feeding hypotheses [25]. Although such behaviours are common among extant great apes, they may not, by themselves, generate the sustained selection pressures required for habitual terrestrial bipedality.

For some researchers, such as Senut et al. [26], specific ecotones like Miombo woodland, with scattered trees and open ground, are thought to have facilitated this transition. Yet vegetation is only one dimension of landscape: tectonically varied terrains have long been recognised as crucial to hominin habitats [e.g., 27, 28]. Tectonic landscapes provide a diversity of terrains and potable water, as well as cliffs that can offer protection, act as barriers to other animals, and serve as conduits for easy movement into adjacent valleys and habitats. Most of these landscapes are associated with the East African Rift System (EARS), which began to form ca. 22 to 25 Ma ago as the Nubian and Somalian plates started splitting apart. The most significant changes have occurred in the Ethiopian region, with massive uplift and rifting progressively transforming this landscape over time, contributing to aridification in the wider region [29].

Ethiopia is a region with an abundance of fossil hominins, coupled with many decades of research and publication starting in the 1930s [reviewed in 30]. *Australopithecus afarensis* was first found in this region in 1976 and published in 1978 [31]. *Ardipithecus* was announced as a separate genus from *Australopithecus* in 1995 [32, 33], and the earliest Homo has been recovered from Ledi-Geraru at 2.8 Ma [34]. In addition, *Paranthropus aethiopicus*, discovered in 1968 [35], represents another hominin species, but one not directly ancestral to early *Homo*.

Ethiopia is also one of the few locations where there is evidence of hominins showing all three inferred types of bipedal behaviours: *Ardipithecus* (facultative), followed by *Australopithecus* (habitual), and finally, later *Homo* (obligate bipedalism). Hominin bipedalism has also been inferred from the skeletal morphology of the femur in *Orrorin tugenensis*, from Tugen Hills in Kenya [13], and from the *Sahelanthropus tchadensis* hominin individual from Toros-Menalla, Chad [17]. While these claims are widely cited, both identifications remain contentious. We do not attempt to resolve these contentious cases here, and they are treated as contextual rather than central to the argument developed below. These settings may not have provided the long-term landscape continuity and refugial protection that, in our model, would be most conducive to the persistence and consolidation of obligate bipedality, although this remains an inference rather than a conclusion. At present, sustained lineage continuity in those regions remains uncertain under the current record.

While this study does not present new fossil material, it uses a GIS-assisted geological and geomorphological synthesis to examine long-standing gaps and patterns in the hominin fossil record. The focus is not hominin anatomy in itself, but the evolving landscape and the ways in which tectonic and geomorphic history may have shaped the evolutionary opportunities available to resident hominin populations. In settings of restricted connectivity, reduced gene flow and strong landscape structure may promote population persistence and local divergence, allowing adaptations to accumulate and be retained over long timescales. Refugia may further buffer populations against environmental variability and recurrent mixing with neighbouring groups. By contrast, transitions to more connected settings may increase exposure to predation, competition, and dispersal, filtering which traits and lineages persist. This perspective is applied here to the development of hominin bipedalism in relation to the landform evolution of Afar and Kenya (Figure 1). Figure 1 summarises the working sequence proposed here: initial connectivity before full Ethiopian Dome and Afar isolation, a prolonged interval of reduced permeability and refugial persistence, and later southward dispersal opportunity as the Main Ethiopian Rift became more throughgoing.

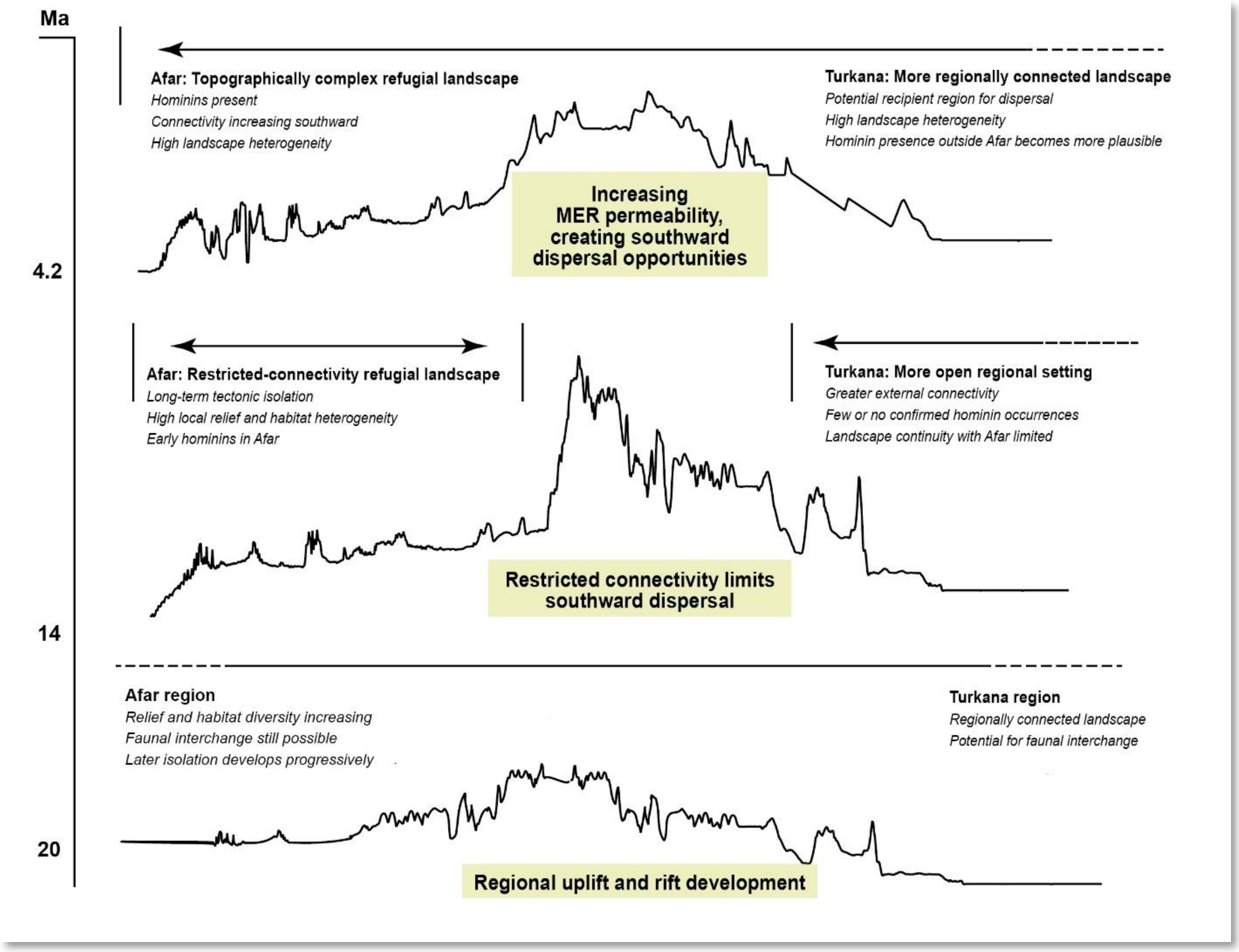

Figure 1. *Landform evolution from 20 Ma to 4.2 Ma. Derived conceptual elevation-profile reconstruction illustrating the major stages of landform evolution and how these may have influenced regional connectivity between Afar and the Turkana Basin. The profile was informed by QGIS elevation profiling of present-day DEM topography, then interpreted against published geological evidence for Ethiopian Dome uplift, Afar development, and Main Ethiopian Rift opening. It is a schematic summary of relative landscape permeability and topographic isolation, not a measured palaeoelevation profile or literal ecological reconstruction.*

This study therefore examines whether long-term geomorphological isolation in Ethiopia may have contributed to the persistence and stabilisation of early bipedal traits before later dispersal into more connected landscapes. Even today, the Ethiopian landscapes possess a high level of endemic species [e.g., 36, 37] due to their topographic diversity and high levels of tectonic and volcanic activity driven by the rifting of a triple junction [38]. This paper argues that the unique landscape evolution of Ethiopia may have created a long-lived setting of restricted connectivity over millions of years, which may have favoured the persistence and stabilisation of early bipedal traits within a terrain-buffered refugial landscape. GIS-assisted landform maps of key temporal stages are used to outline the effects of isolation and migration on ecosystems, and to consider the implications for hominin locomotion and bipedality in Afar and along the Main Ethiopian Rift corridor.

2. STUDY FRAMEWORK AND METHODS

2.1 Study framework

In this study a refugium is a landscape that remains reliably habitable and defensible over long periods, allowing populations to persist through climatic variability with reduced disruption from frequent mixing with neighbouring regions. Refugia can therefore alter population connectivity, and the balance between local adaptation, drift, and gene flow, thereby allowing divergence to accumulate over long timescales [39-41]. A connectivity threshold refers to the point at which a previously segmented landscape becomes passable enough to allow sustained dispersal, not as a single event, but as a broader shift in overall landscape permeability. The study examines whether the available evidence is consistent with a model in which Afar’s long-lived tectonic and geomorphological evolution created refugial conditions favouring the persistence of early bipedal traits, and whether later changes in rift structure enabled dispersal once connectivity thresholds were crossed.

2.2 Data sources, locality records, and analytical extract

The hominin fossil locality component of this study derives from a broader private research database compiled by the lead author, covering African and Arabian hominin fossil, archaeological, geological, and palaeoenvironmental locality records. Only a restricted analytical extract from that database has been used here, focused mainly on selected early hominin records up to and including *Australopithecus*, together with selected geological, palaeoenvironmental, and formation localities relevant to Afar, the Main Ethiopian Rift, Mursi, and the Omo-Turkana Basin.

Each plotted hominin fossil locality in the relevant figures corresponds to a source-checked database entry, with taxonomy, age, locality name, formation or site context, geographic position, landscape and rift context, and source information harmonised against the cited literature where possible. The extract was designed to support spatial comparison and figure construction, not to provide a complete census of fossil occurrences or a formal statistical analysis of diversity, absence, or abundance. Apparent gaps in the record are therefore treated as constraints requiring geological and taphonomic context, rather than as direct evidence of biological absence.

2.3 GIS synthesis and figure construction

This study presents a GIS-assisted tectonic and geomorphological synthesis of the Afar region and the Main Ethiopian Rift using time-sliced conceptual reconstructions. Published geological maps, regional stratigraphic and tectonic syntheses, and modern topography are integrated in a GIS environment to visualise how rift structure, relief, and basin geometry evolved through key intervals, and to compare these changes with the spatial distribution of major fossil localities. The GIS component is used to collate, georeference, and display spatial relationships, and to support consistent mapping across stages, rather than to perform quantitative route modelling or least-cost path analysis.

Figures 3 to 7 are original schematic reconstructions derived from published tectonic, geomorphological, palaeogeographic, drainage, and fossil-locality evidence. Figures 8 and 9 are QGIS-generated maps using selected locality records, DEM-derived topography, and published geological or rift-structure information. The clean visual form of these figures reflects distillation from the underlying data compilation and mapping process, rather than simple illustrative redrawing.

The staged reconstructions were developed as source-led, backwards-constrained interpretations rather than as fixed quantitative palaeogeographic models. For each interval, the reconstruction was limited by the availability of published tectonic, palaeogeographic, drainage, and rift-evolution studies relevant to that time slice. These published interpretations were then compared with present-day geographic anchors, including Lake Tana, the Blue Nile, the Danakil Block, the Triple Junction, the Afar Depression, and the Middle Awash locality system, to maintain spatial consistency when moving backwards through successive landscape configurations.

Where the published record did not support a more precise reconstruction, the figures were kept schematic and interpretive rather than predictive. This source-led approach was especially important for evaluating the changing position of the eventual Middle Awash locality system in relation to Danakil Block separation, Afar development, and later Main Ethiopian Rift connectivity. Figure 7 then uses modern topography and published geological relationships to summarise the staged opening of the Main Ethiopian Rift, while Figures 8 and 9 add the locality dataset and published rift-structure information to examine the spatial relationship between hominin localities, the MER, and the Turkana Basin rift framework.

The outputs are a set of stage maps and schematic diagrams that highlight changing isolation, barriers, and corridor permeability, and provide a framework for discussing refugial persistence and later dispersal as connectivity thresholds were crossed.

To make the evidential structure of the synthesis explicit, Table 1 summarises how the main evidence components, figures, and interpretive steps relate to one another.

Table 1. Summary of main evidence components, figures, and interpretive steps

Evidence component	Principal inputs	Manuscript output	Interpretive role
Staged tectonic and geomorphological reconstructions	Published geological, tectonic, palaeogeographic, drainage, and rift-evolution studies	Figures 3–7	Reconstruct changing isolation, basin development, drainage reorganisation, and corridor permeability through time
Fossil and locality extract	Source-checked records from the restricted analytical extract, including taxon, locality, age, formation or site context, coordinates, landscape and rift context, and primary sources	Supplementary Table S1, Figure 8	Provides the locality basis for comparing Afar, Mursi, Omo-Turkana, and selected wider regional records
Regional fossil comparison	Selected Miocene ape and early hominin records from Ethiopia, Kenya, and Tanzania	Table 2	Places early hominin occurrences in broader regional and chronological context
Rift-structure and locality overlay	Selected early hominin localities, DEM-derived topography, and published rift-structure reconstructions	Figure 9	Evaluates the spatial relationship between key early hominin localities and rift-margin or basin-margin structures
Refugial-connectivity interpretation	Combined tectonic timing, landscape structure, locality distribution, and fossil-record constraints	Discussion, especially Section 4.4	Assesses whether the evidence is consistent with a refugial-connectivity scenario, while identifying alternative explanations and revision triggers

This structure is intended to clarify the distinction between observed or source-derived evidence, GIS-assisted spatial comparison, and the working evolutionary interpretation developed in the Discussion.

2.4 Scope and limitations

This paper does not attempt to resolve taxonomic disputes or re-evaluate individual fossil specimens. Instead, it focuses on landscape-scale mechanisms, tectonic isolation, geomorphological structure, and connectivity thresholds, and evaluates whether the available evidence is consistent with these factors structuring hominin persistence and dispersal. Alternative narratives, including climate-driven habitat change, savannah expansion, and behavioural or anatomical triggers, remain relevant, but by themselves they do not address how long-term tectonic landforms control habitat continuity, access to refuge terrain, and the practical routes available for dispersal. In particular, models that focus mainly on vegetation change or anatomy often do not explicitly consider the behavioural constraints of predator avoidance and safe nocturnal refuge, including the availability of defensible sleeping sites, which are directly structured by terrain and relief. This paper evaluates landscape-scale mechanisms and does not require a single habitat type or a single ecological regime, and wooded and mosaic settings remain compatible with the scenario.

A working dispersal scenario from Afar is evaluated against the current fossil record, but is not presented as proof derived from first appearances or record gaps. Non-recovery of hominins, including at Mursi, is treated as potentially informative where it has been identified as noteworthy in the literature, but not as proof of true biological absence. Such patterns require comparison with sampling, preservation, exposure, and depositional context.

This scenario can be tested and revised as new geological, chronological, and fossil evidence becomes available. Quantitative route modelling is not attempted here.

3. RESULTS

The GIS-assisted reconstruction identifies a sequence of major tectonic and geomorphological changes relevant to hominin persistence and dispersal in East Africa, with particular emphasis on the Afar region and adjacent Main Ethiopian Rift. These results derive from the integration of published tectonic and geomorphological syntheses, DEM-derived topographic context, and selected source-checked locality records described in Section 2.2. The reconstructed sequence includes prolonged phases of regional isolation, progressive reorganisation of rift structure and drainage, and the later development of more permeable southward connections. The principal spatial and chronological patterns identified through this synthesis are presented below, followed by their implications for interpreting the Mursi Formation and the Omo-Turkana Basin fossil record.

3.1 Landform evolution in East Africa

The reconstruction indicates that landform evolution in East Africa proceeded through a series of major tectonic stages that progressively altered isolation, drainage structure, basin development, and corridor permeability. These stages provide the spatial and temporal framework used here to assess refugial persistence in Afar and the later opening of southward dispersal routes.

3.1.1 Stage A: Island Africa, ca. 110 Ma to ca. 25 Ma

This stage is characterised by prolonged isolation of Afro-Arabia, with no sustained land connection permitting major faunal exchange until the approach to the Great Old World Biotic Interchange at around 20 Ma (Figure 2).

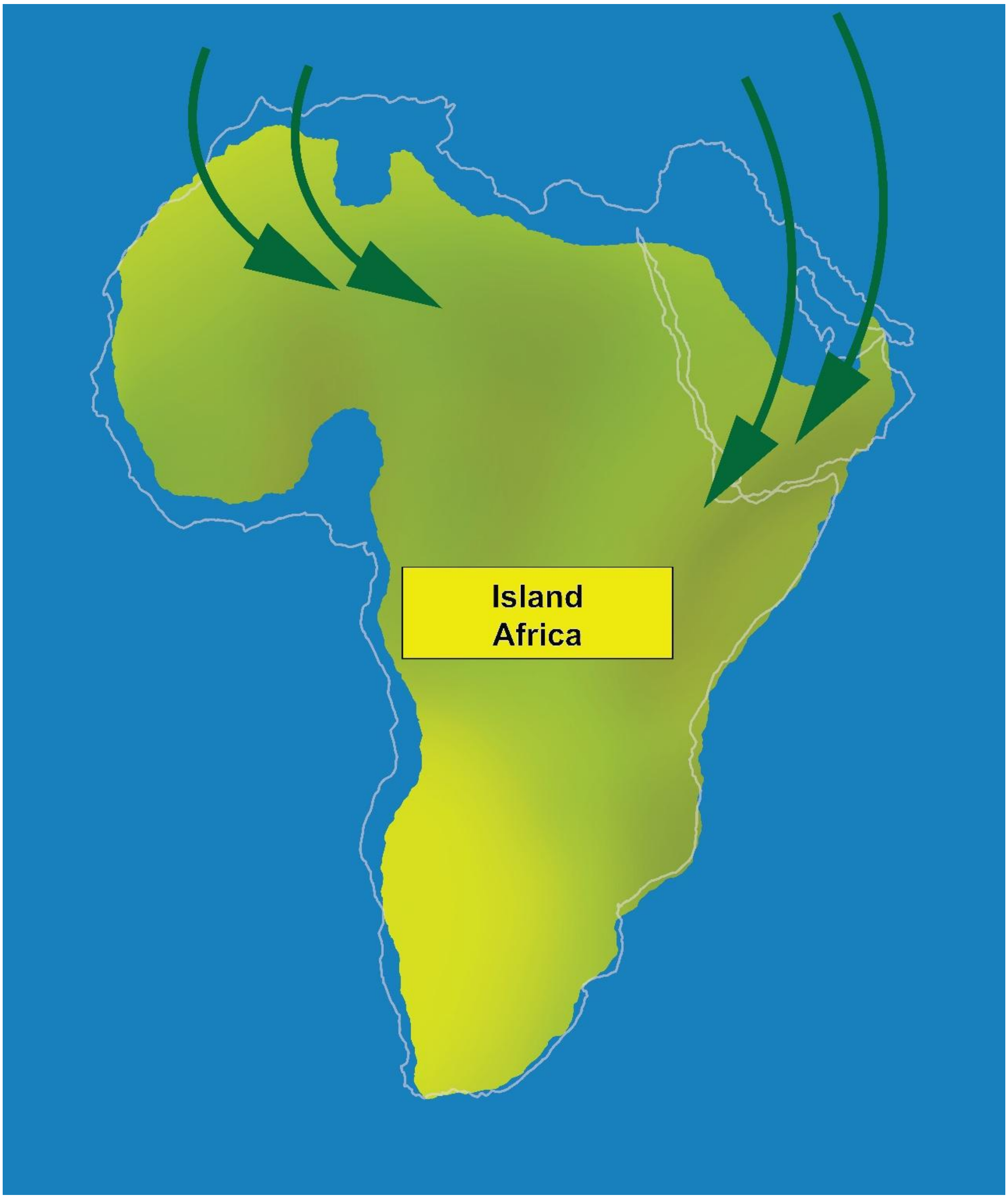

Figure 2. *Stage A: Island Africa ca. 110 Ma to ca. 25 Ma. Literature-derived palaeobiogeographic context figure showing selected Eocene trans-Tethyan mammalian dispersal events into and out of Afro-Arabia during the long interval of partial isolation before Miocene land connection. Arrows denote migratory phases prior to and leading up to the Great Old-World Biotic Interchange (GOWBI) between Eurasia and Afro-Arabia at around 20 million years ago [modified and redrawn after 42].*

The “Island Africa” emerged after separating from South America roughly 110 Ma and, for reasons that are still unclear, exhibited poor species diversity from the outset [43, 44]. There was therefore very little faunal exchange with other continents and this species paucity, and the concomitant growth in endemic taxa, continued until the approaching closure of the Tethys Sea, which finished during the Miocene epoch. Little is known about the fauna inhabiting Africa during this long interval of isolation, but one notable legacy of Afro-Arabian isolation is the endemic placental clade Afrotheria, represented today by six orders, Proboscidea, Sirenia, Hyracoidea, Macroscelidea, Tubulidentata, and Tenrecoidea [45, 46]. Molecular estimates place the origin of this clade between 74.4 and 96.5 Ma [47], but the fossil record of this time period remains poor. From 56 Ma, Island Africa moved closer to Eurasia, at a rate of 2-3 cm per year [42, 48], and while these land masses were still isolated, important sweepstakes dispersals took place (rodents, primates, embrithopods and elephantids to name a few) into Island Africa. The so-called *Gomphotherium* landbridge formed when the two continents finally connected around 20 Ma, initiating a major faunal migration, known as the Great Old World Biotic Interchange (GOWBI) [44, 45, 49]. Groups of animals that moved from Africa into Europe included proboscideans, hyracoids and tubulidentates [e.g., 45], while in the opposite direction, the pulses of vertebrate expansion into Afro-Arabia are thought to explain the evolutionary success of many of their descendant species in Africa today [44].

Molecular divergence rates for primate clades give a Last Common Ancestor (LCA) for crown primates of around 66 million years ago [e.g., 42, 50] and therefore suggest that they arrived in Africa from Laurasia (Europe + Asia). By 34 Ma, however, there existed a wide array of primate lineages on the Afro-Arabian continent that experienced multiple competitive phases due to migrations across the Tethys Sea during ‘chance dispersals’ before the GOWBI [42]. These dispersals were primarily into Africa; either via northwest Africa or Arabian routes (Figure 2). The main Palaeogene primate-bearing fossil sites in Morocco, Algeria, Libya, Tunisia, Egypt, Saudi Arabia, and Oman imply such possible migratory routes [42 and references within, 43].

The relevance of Stage A to the present study is therefore not direct hominin history, but the establishment of a deep-time biogeographic pattern in which African faunas were repeatedly structured by isolation, episodic dispersal, and changing land connections.

3.1.2 Stage B: Plume uplift, ca. 32 Ma

This stage marks the incipient formation of the Kenyan and Ethiopian domes. Mantle upwelling beneath East Africa had begun and would eventually contribute to the development of both domes [51]. Figure 3 shows a reconstruction of the Afro-Arabian region at approximately 32 Ma.

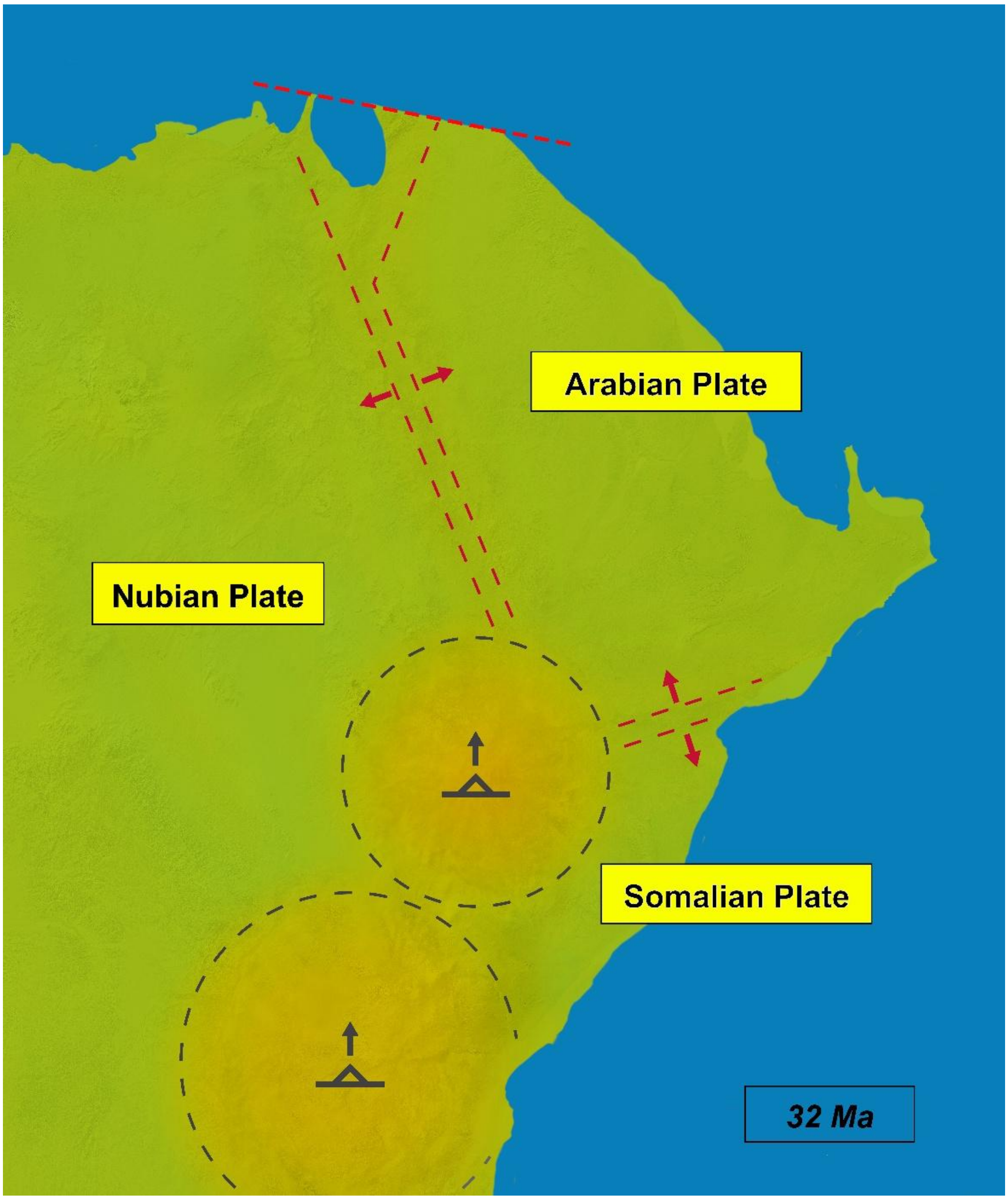

Figure 3. *Stage B: Plume uplift at 32 Ma. Literature-derived schematic reconstruction of Afro-Arabia at approximately 32 Ma, based on published geomorphological and palaeogeographic interpretations. The beginning of the Ethiopian and Kenyan domes can be seen [after 51]. The incipient rift zones associated with the later development of the Red Sea and the Gulf of Aden are indicated schematically.*

The African Superswell uplifted the majority of the African continent to above 1 km in elevation during this interval [52, 53]. The uplift and erosion initiated at this time have continued since, and

Gani and Neupane [54] suggest that the uplift of the Ethiopian Plateau continues to the present day. This uplift has been implicated in the development of grassland-dominated habitats thereafter [e.g., 29]. Over the past 32 million years, there has been additional mantle plume uplift of between 1 and 2 km [55, 56] supplemented by the deposits of up to 4 km of various volcanic layers [57, 58].

As these landform changes were taking place ca. 32 million years ago, direct environmental evidence from East Africa is limited, so well-described African localities of comparable age are used here as illustrative context rather than as regional proxies. One such example is the vertebrate fauna from Birket Qarun Locality 2, BQ-2, within the Jebel Qatrani Formation in Egypt [59-62]. The evidence indicates that this was predominantly a freshwater ecosystem, dominated by fish species [e.g. catfish, 63]. The Jebel Qatrani Formation, dated to between 35.4 and 33.3 million years ago [64], is dominated by aquatic bird species such as the jacana, cranes and the shoe-billed stork [65], but also by primitive prosimians, such as *Wadilemur elegans* [60]. Taken together, the avifauna and aquatic taxa indicate wetland or swamp mosaics with wooded margins, broadly comparable to some modern African freshwater systems. Fish and reptile evidence indicates periodic inundation and desiccation, including catfish and lungfish, and reptiles such as spiny-tailed lizards [66-68]. These assemblages are cited to indicate that freshwater wetland mosaics bordered by forest and woodland were widespread habitat types in Africa long before hominins. No direct habitat continuity is implied between these Oligocene settings and later hominin localities. Rather, the recurrence of freshwater-linked mosaics provides useful ecological context for later Plio-Pliocene localities, where springs, wetlands, and lake margins again become important components of primate and hominin landscapes [69, 70].

Against this background of long-standing freshwater-linked mosaics, the principal result of Stage B is that plume uplift and early dome growth began reorganising East African topography and drainage in ways that later constrained connectivity and dispersal routes.

3.1.3 Stage C: Active rifting, ca. 27 Ma

At ca. 27 Ma, Afro-Arabia was continuing to converge on Eurasia, and the landscape processes are dominated by the active rifting in regions of the present-day Red Sea and Gulf of Aden (Figure 4). Published estimates for the onset of this rifting vary, with some placing it near 30 Ma [71], and others closer to 24 Ma [72].

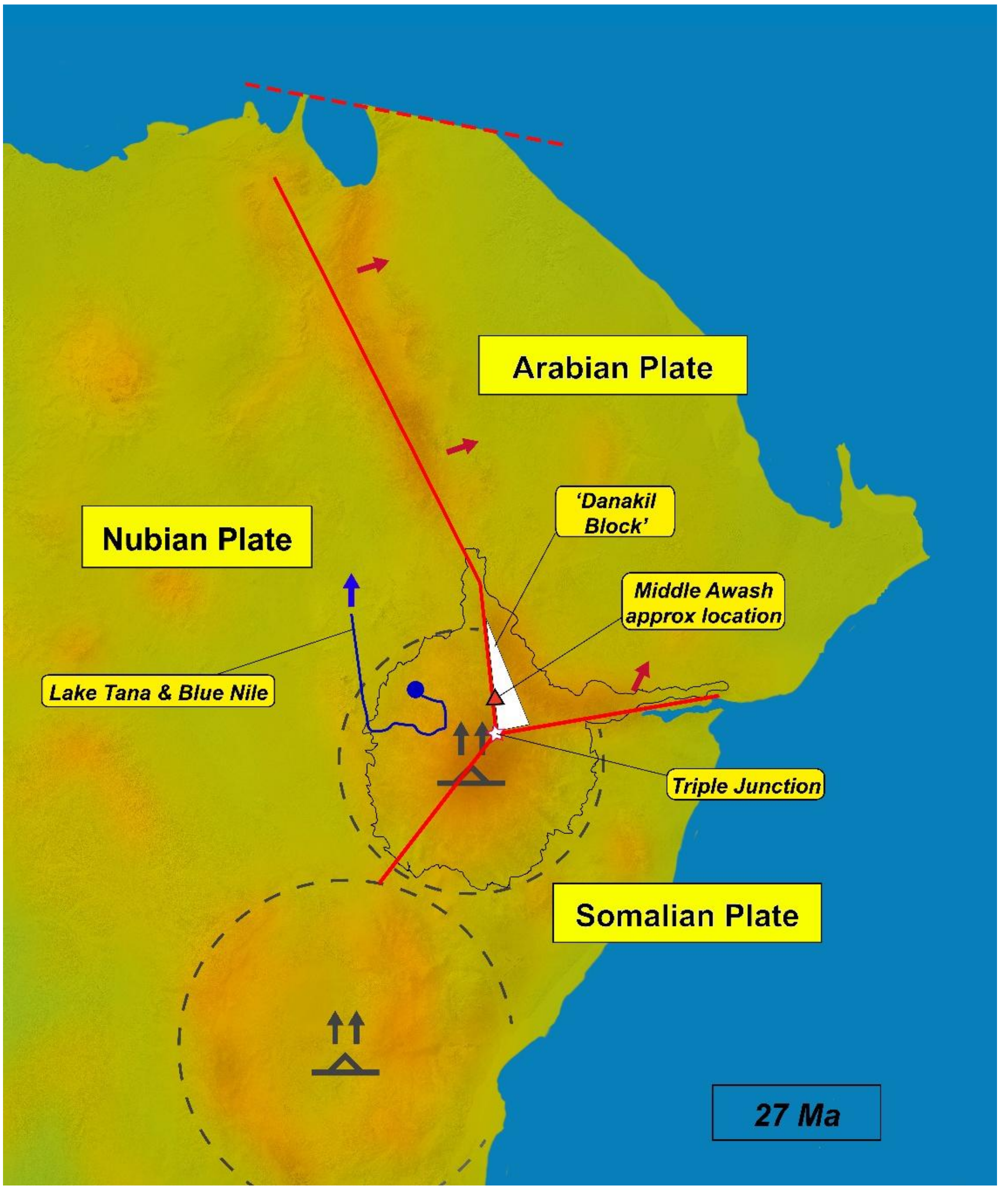

Figure 4. *Stage C: Active rifting 27 Ma. Literature-derived schematic reconstruction of Afro-Arabia at approximately 27 Ma, based on published geomorphological, tectonic, and palaeogeographic interpretations. The locations of the Ethiopian and Kenyan plumes, domes, are shown [after 51]. Rifting (red lines) emanating from the Triple Junction is beginning to partition the Ethiopian Dome to form what will eventually be the Red Sea, the Gulf of Aden, and the Ethiopian Rift Valley. The Afar does not yet exist; neither does the Danakil Block [71]. The approximate location of the eventual Middle Awash research area is indicated for orientation, although the modern fossil-bearing landscape and locality system had not yet formed in its present geomorphic configuration. The white triangle signifies the area likely to become the Danakil Block. The small white star denotes the approximate Triple Junction location. The eventual locations of Lake Tana and Blue Nile are also shown as geographic reference points for orientation, not as literal reconstructions of their modern form at 27 Ma.*

According to Zwaan et al. [73], rifting in the Gulf of Aden began as early as 35 Ma and was followed by oceanic spreading at 17-20 Ma before moving westward towards Afar. Erosion initiated the Blue Nile Canyon (Figure 4), probably as early as 25–29 million years ago [55, 74, 75], which led to incisions/canyons of up to 1.6 km deep and remains a major source of the River Nile even today. There remains some debate on the northerly route of the river over that timescale [e.g., 74, 76-78].

Habitat conditions at 27 Ma are indicated by sites such as Chilga (1950 masl) to the north of Lake Tana, Ethiopia, which boasts an impressive faunal assemblage that is quite unlike the faunal communities of later time periods in this region. The fauna is dominated by a range of extinct proboscideans, hyracoids and a species of rhinoceros-like embrithopod*, Arsinoitherium giganteum* [79, 80]. The present-day Middle Awash region (Figure 4) was both inland and in an area dominated by active rifting, as the three plates (Arabian, Nubian and Somalian) diverge. The Red Sea eventually develops to the east of (what will be) the Danakil Block (Figure 4). The Middle Awash region to the west of the Danakil Block would have contained features associated with active rift margins, which include wetlands, cliffs, and heterogenous environments. Such settings later become prominent in early hominin landscapes, because they provide fresh water, diverse food resources, and predator refuge in the form of cliffs and roosts [e.g., 27, 28, 81].

The Oligocene-Miocene boundary (ca. 23 Ma) is associated with important evolutionary changes where several current lineages of mammalian Orders, including Primates, emerged from sites in the Turkana Basin [79, 80, 82]. Multiple sites in the Lake Turkana area have been investigated [82], and Oligocene sites such as Lokone are of a similar age to Chilga (Ethiopia) and Dogali (Eritrea), ca. 26-28 Ma. The Lokone mammals show strong taxic affinities to the material preserved at Fayum in Egypt, yet show fewer affinities to the younger (Miocene) material in the Turkana Basin or elsewhere in East Africa, which suggests that a later faunal turnover occurred [82]. Despite the presence of primates in the Lake Turkana basin, the well-stratified and fossil-rich Nawata Formation at Lokone has no securely dated hominin fossils before 5 Ma, based on the published record, as indicated by Leakey et al. [82]. They noted that "…it is surprising, and perhaps significant, that hominins are absent until a time close to 5 MYA. Monkeys, on the other hand, are relatively common in the Nawata Formation" [82: 250]. We suggest, as a working possibility, that the first hominin occurrences soon after 5 Ma may relate to increasing landscape connectivity southwards, including along the developing MER.

The principal result of Stage C is that active rifting had begun to partition the Ethiopian region, reorganise drainage, and establish the tectonic framework from which the Afar Depression and later Main Ethiopian Rift corridor would develop.

3.1.4 Stage D: Danakil plate movements and Afar Depression initiation, ca. 14 Ma

This stage marks the beginning of relative separation of the Danakil Microplate from the Nubian Plate, a tectonic reorganisation that contributed to the later development of the Afar Depression (Figure 5).

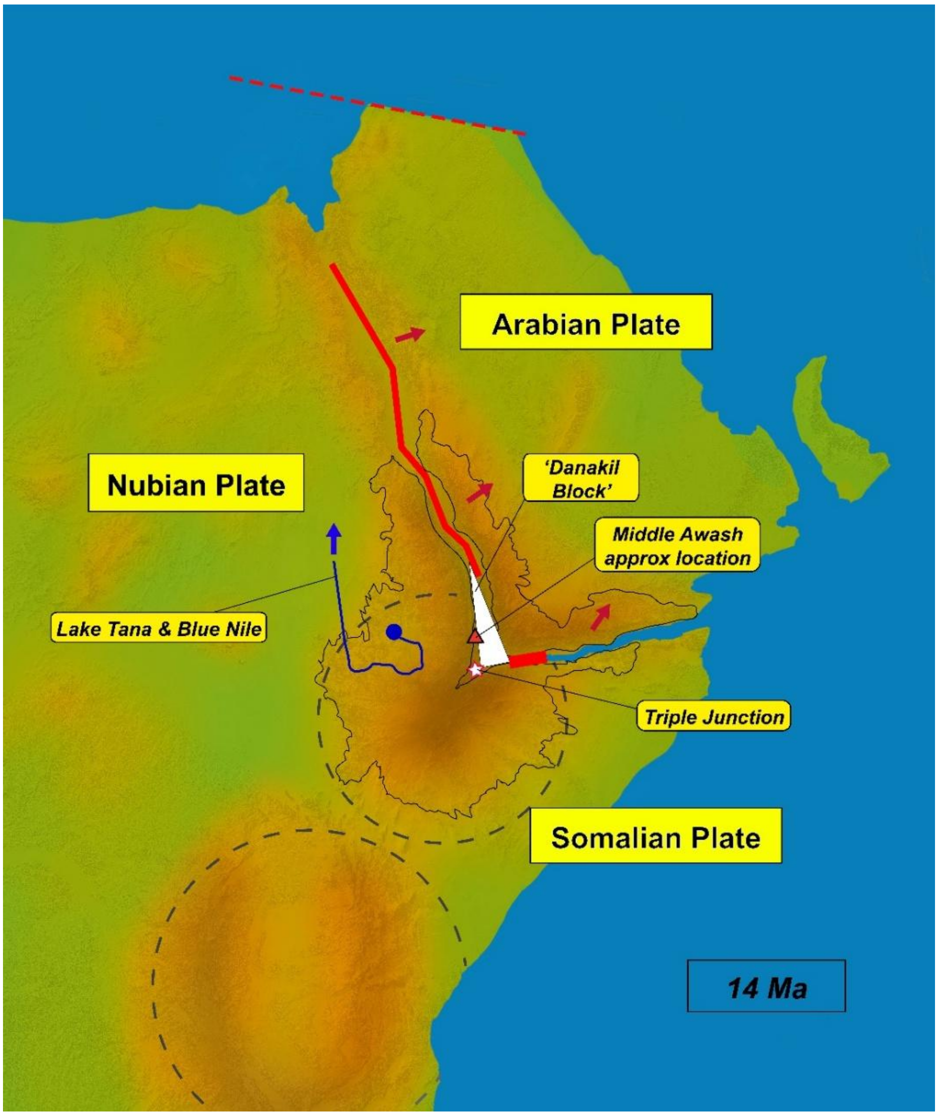

Figure 5. *Stage D: Danakil plate movements and initiation of Afar Depression at 14 Ma. Literature-derived schematic reconstruction of Afro-Arabia at approximately 14 Ma, based on published geomorphological, tectonic, and palaeogeographic interpretations, cross-checked against modern geographic relationships for spatial orientation. The locations of the Ethiopian and Kenyan plumes, domes, are shown [after 51]. Continued rifting (red lines) has extended the Gulf of Aden from the Indian Ocean, but the Red Sea seaway has not yet formed. Rifting to the west of the Danakil Block has been replaced by more intense rifting to the east, and soon to become the Red Sea [71]. The Afar Depression had not yet formed, but the Danakil Block has started separating from the Nubian Plate. Prior to 14 Ma, the Danakil Microplate was attached to the Nubian Plate, with separation from the Arabian Plate starting at 13 Ma [71, 72]. The approximate location of the eventual Middle Awash research area is indicated for orientation, although the modern fossil-bearing landscape and locality system had not yet formed in its present geomorphic configuration. The white triangle signifies an area likely to become the Danakil Block. The small white star denotes the approximate Triple Junction location. The eventual locations of Lake Tana and Blue Nile are also shown as geographic reference points for orientation, not as literal reconstructions of their modern form at 14 Ma.*

Prior to 14 Mya, the Danakil Microplate was attached to the Nubian Plate [described as a ‘close fit’ by 71], with the separation from the Nubian Plate possibly starting ca. 13 Mya [71, 72], or 11 Mya [83]. This separation of the Danakil Microplate from the Nubian Plate will eventually lead to the formation of, in time, the Afar Depression. Rifting in the Red Sea started at 30 Ma [71] with seafloor spreading in the Central Red Sea and Southern Red Sea dated to around 5 Ma, though it might have started as early as 12 Ma [73]. In the Gulf of Aden, oceanic spreading started at 17.6 Ma (or possibly even 20 Ma in the far east of the Gulf of Aden) and then moved westward towards Afar. Rifting to the west of the Danakil microplate is replaced by intense rifting to the east. The short initial phase of N–S strike-slip fault at 27 Ma between Arabia and Nubia (to the west of the Danakil microplate) was replaced by the development of NW–SE normal faults to the east of the Danakil microplate [71]. The net result of these different phases of extensional and strike-slip faulting is the formation of the Afar Depression, and the eventual fusion of the Red Sea with the Gulf of Aden [71].

At this stage, the Danakil Block remains largely intact, but it has begun shifting position relative to both the Nubian and Arabian Plates. The Afar Depression has not yet formed, but the tectonic processes that will eventually create it are now underway. The principal result of Stage D is that reorganisation around the Danakil Microplate had begun to establish the tectonic framework from which the Afar Depression would later develop.

3.1.5 Stage E: Development of the Afar Depression, ca. 13-5 Ma

The rotation of the Danakil microplate (Figure 6) was initiated at 13 Ma and was completed by 5 million years ago [72], although Zwaan et al. [83] suggested a slightly later start for this event at 11 Ma.

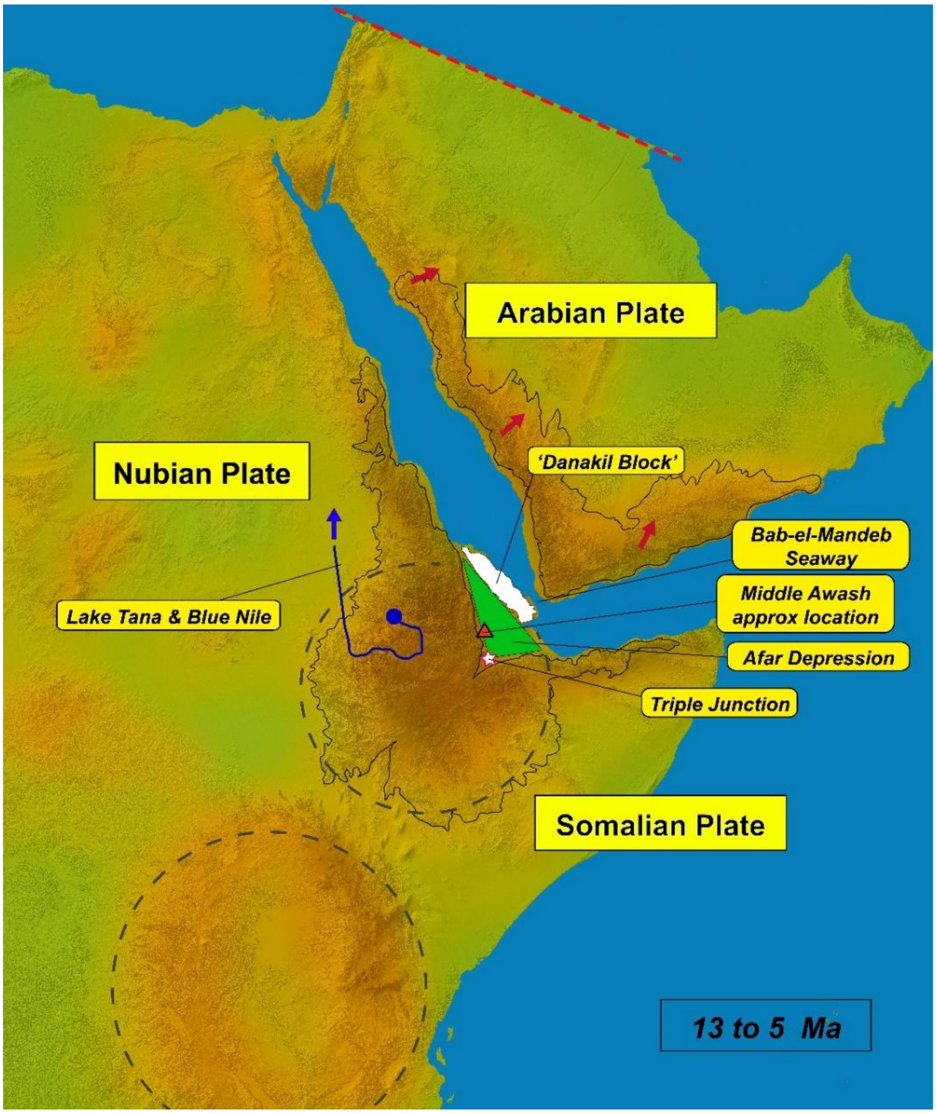

Figure 6. *Stage E: Development of the Afar Depression at 13-5 Ma. Literature-derived schematic reconstruction of Afro-Arabia during the interval ca. 13 to 5 Ma, based on published geomorphological, tectonic, and palaeogeographic interpretations, cross-checked against modern geographic relationships for spatial orientation. The locations of the Ethiopian and Kenyan plumes, domes, are shown [after 51]. The rotation of the Danakil Block started at 13 Ma [72] or 11 Ma [83] and was completed by 5 Ma. The location of the Bab-el-Mandeb land bridge, and its subsequent replacement by the Bab-el-Mandeb seaway at 5.3 Ma, is shown. The approximate location of the eventual Middle Awash research area is indicated for orientation within this evolving landscape, rather than as a literal reconstruction of the modern fossil-locality system. The small white star denotes the approximate Triple Junction location. The eventual locations of Lake Tana and Blue Nile are also shown as geographic reference points for orientation, not as literal reconstructions of their modern form throughout the 13 to 5 Ma interval. Because this figure represents an interval rather than a single moment, it should be read as a time-averaged schematic of changing isolation and seaway development, based on published tectonic models with differing chronological interpretations.*

Formation of the Bab-el-Mandeb seaway marked a major tectonic and biogeographic transition, connecting the Red Sea to the Gulf of Aden and fully separating the Afar region from the Arabian Peninsula. Estimates for this event range from 6.2 to 4.5 Ma [84] to 5.3 Ma [85] when oceanic spreading in the Southern Red Sea initiated an influx of seawater into the Red Sea basin through the Bab-el-Mandeb seaway.

Even prior to the Bab-el-Mandeb seaway incision, the Red Sea basin would have posed a formidable migration barrier to species. There has been a continual process of sea influx followed by water evaporation over the period 12–5 million years ago prior to this, making the environment one of extensive evaporite deposition [85-87], which would be a challenging area to cross for many species. Crossing between Arabia and Afar was therefore likely to have become increasingly restricted during this interval.

The existence of a land bridge between Afar and the Arabian Peninsula during this period explains the closely related taxa and species migrations between the Horn of Africa and Arabia in the Miocene [84, 88 and references therein, 89]. Examples include various freshwater fish, gecko, monitor lizard, terrapin, extinct elephants, vipers and cobras. Studies of the late Miocene Baynunah Formation, Abu Dhabi, exposed a 6.5 to 8.0 Ma fossil guenon that represents the earliest cercopithecine (and only guenon) yet known outside of Africa [90, 91]. The dispersal scenarios for cercopithecoid primates out of Africa and through Arabia suggest that the land bridge was a probable route into Asia. There is much speculation about where hominins originated (Africa, Asia or even Europe), but the present study follows Harrison [92] in treating Africa as the most likely region of hominin origin.

At around 5.3 Ma, the Bab-el-Mandeb land bridge disappears, and the Afar Depression, including the Middle Awash area within it, would have become increasingly isolated from Arabia and adjacent regions [84]. The depression is bounded by steep, uplifted, rift flanks to the south and to the west, and by the Danakil Block and the Red Sea to the east (Figure 6). To the North lies the Levantine corridor, which is the only migration corridor between Africa and Eurasia [e.g., 89]. By this time, the Middle Awash region had been located in a region of active rifting for upwards of 25 million years. These tectonic developments increased regional isolation and strengthened the restricted-connectivity character of the Afar basin.

The earliest hominins relevant to this study appear in the record during this interval, with *Ardipithecus kadabba* at around 6.3 Ma and *Ardipithecus ramidus* at 4.4 Ma [32, 93, 94]. Palaeoenvironmental reconstructions indicate that the habitats associated with these earliest hominins were largely wooded in character [93, 94], although some isotopic studies suggest greater openness [95]. The species most commonly recovered with *Ardipithecus ramidus* are generally other species of smaller monkeys and tragelaphin antelopes, which together suggest a wooded environment. The relatively low numbers of recovered carnivore species are of particular interest in the Awash region, as these were the potential predators of hominins and other medium-sized mammals. The Awash region between 13-5 Ma includes only two genera of saber-toothed cats, namely *Dinofelis* and *Machairodus*, two hyaenids (*Ikelohyaena abronia* and *Crocuta* cf. *dietrichi*), as well as the ursid genus *Agriotherium* and the canid genus *Eucyon* [96]. There are signs that the fossil remains associated with the *Ardipithecus ramidus* assemblage were carnivore-ravaged but with a relatively modest number of carnivore species represented [93, 96]. This contrasts with the richer predator guilds documented at some later hominin localities, including Pliocene Sterkfontein [97]. The majority of the carnivoran guild at that time was composed of small viverrids and aquatic fauna, such as otters, which would not typically have preyed on adult Ardipithecus-sized mammals, estimated at about 50 kg [93, 98].

The principal result of Stage E is that development of the Afar Depression, together with loss of the Bab-el-Mandeb land bridge, created a more isolated and terrain-structured basin in which the earliest *Ardipithecus* records appear under restricted-connectivity conditions.

3.1.6 Stage F: Formation of the MER, ca. 5 Ma

This stage marks the development of the Main Ethiopian Rift, MER, from a segmented rift system toward a connected throughgoing southward corridor, with increasing potential for faunal movement between Afar and the Turkana Basin. In the period leading up to 5 Ma, the region experienced continued mantle plume activity, which likely further uplifted the Ethiopian Plateau [74]. Given the varied tectonic timings, magmatic histories, and underlying lithospheric properties of the region, the Main Ethiopian Rift is commonly divided into three distinct sections, the Northern MER, the Central MER, and the Southern MER, and explanations for its development require consideration of each [99-102] (Figure 7).

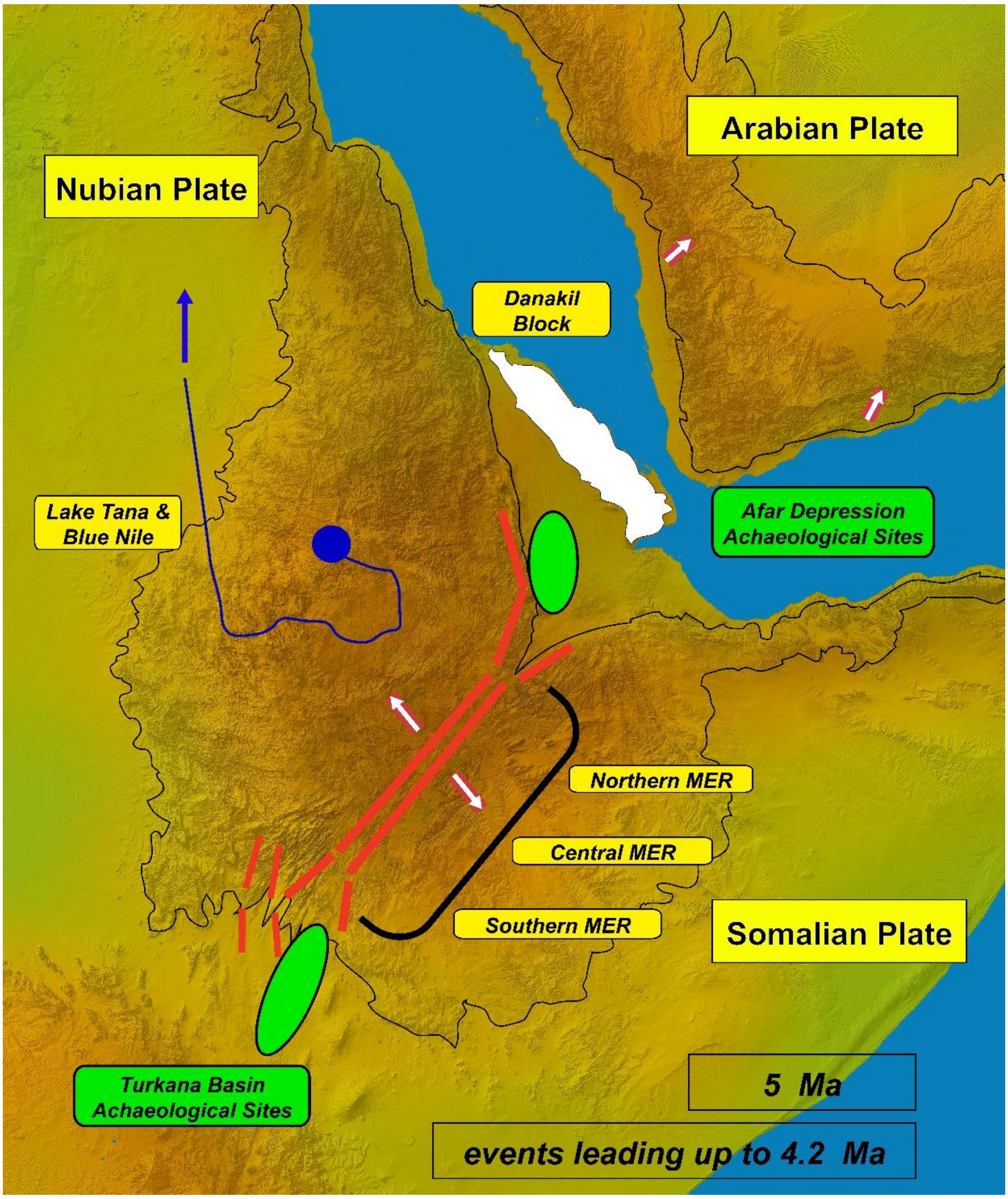

Figure 7. *Stage F: Formation of the MER at ca. 5 Ma. GIS-assisted reconstructed map of Afro-Arabia around 5 million years ago, showing the Northern, Central, and Southern MER segments and the principal fossil localities discussed in the text. The figure combines present-day geographic reference points, including Lake Tana and the Blue Nile, with published tectonic interpretations and selected fossil-locality data in order to show the approximate spatial relationship between Afar, the developing Main Ethiopian Rift, and the Turkana Basin. The true Danakil Block, Afar Depression fossil localities, and Turkana Basin fossil localities are shown in their approximate positions. Generalised rifting is indicated at either end of the MER, and the map highlights the proposed southward corridor linking Afar to the Turkana Basin. Aspects of localised rift development and the timing of individual tectonic phases remain debated, but published models broadly agree that the Central MER was the last major segment to open.*

There are varied interpretations of these events and their timing, though Keir et al. [102] and Abebe et al. [100] suggest that the Central MER was the last section to experience rifting and therefore the step that enabled the MER to become a more throughgoing rift corridor as indicated in Figure 7. The exact estimates for the date of this event differ among authors, with some suggesting an age younger than 8 Ma [100], others between 5 and 6 Ma [101], 5.2 Ma [74], and around 5 Ma [103]. New geochronological data from the Central Main Ethiopian Rift [104] indicate a major phase of explosive volcanism in the early Pliocene, following a long interval of relative quiescence.

This tectonic and magmatic reorganisation is broadly coeval with early hominin sites in Afar and the Turkana Basin, and is consistent with the interpretation that the Central MER was the late-developing segment whose reorganisation increased southward connectivity. Although future fossil discoveries or revised chronologies may extend the timing of hominin dispersal earlier than 4.2 Ma, ca. 4.2 Ma is treated here as a provisional working horizon given current chronological constraints and gaps in the fossil record.

By the Pliocene, the Kulal, Marsabit, Nyiro, and Ndoto mountains formed a chain of high-relief nodes, enhancing connectivity from the Ethiopian Plateau margin of the Central Main Ethiopian Rift into the northern Kenya rift-shoulder massifs [103, 105, 106]. This configuration provides a plausible stepwise pathway for southward dispersal of montane, cover-dependent vertebrates, including small mammals, without requiring basin-wide climatic humidification. Later dispersal patterns in such taxa are important here, not because they date the earliest hominin movement directly, but because they suggest that this rift-shoulder system could function as a broader biogeographic corridor once southward permeability increased, with different taxa likely responding to this changing permeability at different times and spatial scales.

Taken together, Stage F suggests that the late reorganisation of the Central MER may have established a more continuous southward corridor linking Afar with the Turkana Basin, providing a plausible rift-structured route for dispersal by ca. 4.2 Ma.

3.2 Mursi Formation and implications for dispersal timing

The period prior to 4 Ma is important in hominin evolution, marking the transition from *Ardipithecus* to *Australopithecus*. If the former is indeed a direct ancestor of the latter, then speciation may have occurred over a relatively short interval between about 4.4 Ma and 4.2 Ma [107]. The Mursi Formation in the Omo Valley spans this period and therefore provides an important setting in which to examine dispersal timing. This important site region falls outside of the Afar region of Ethiopia and to the south of the Main Ethiopian Rift (MER) (Figure 8). Chronological estimates for the Mursi Formation vary: including 4.05 to 4.25 Ma [108], greater than 4 Ma [107], 4.0 to 4.5 Ma [109], and 4.5 Ma as the onset of the Mursi Formation's sedimentation [Brown and de Heinzelin, 1983, cited in 107]. Taken together, these estimates place the formation broadly between 4.0 and 4.5 Ma.

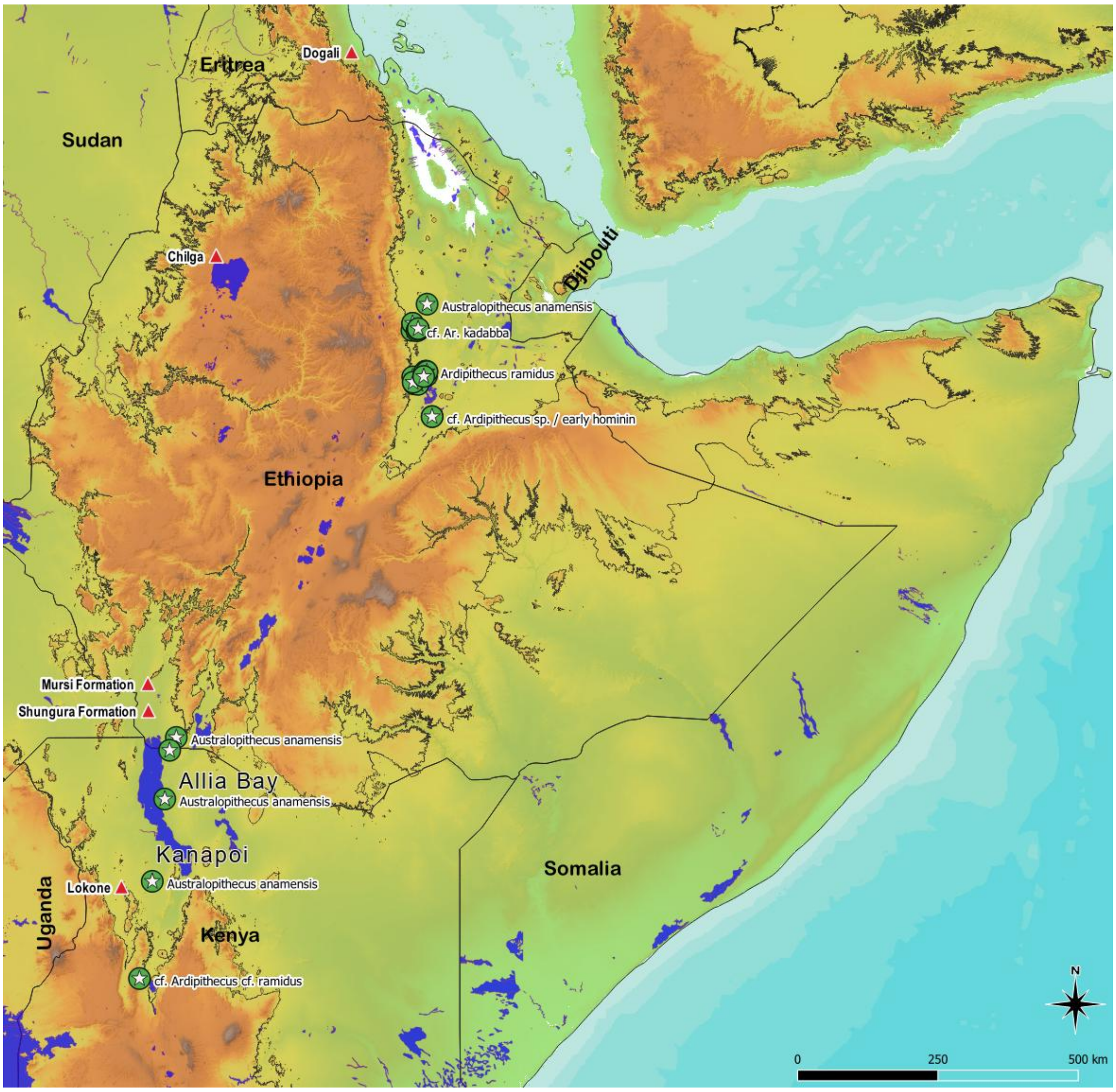

Figure 8. *Major hominin and formation sites in Omo-Turkana Basin and Afar Depression. QGIS-generated present-day topographic map of East Africa showing selected hominin, formation, and palaeoenvironmental localities discussed in the text. The figure was constructed from DEM-derived topography and a restricted analytical extract of source-checked locality records, including key hominin sites and selected geological or palaeoenvironmental reference localities such as Lokone, the Mursi Formation, the Shungura Formation, Allia Bay, Kanapoi, Chilga, and Dogali. It is intended to show their relative spatial proximity and position with respect to the Main Ethiopian Rift. The locations of Ardipithecus and Australopithecus anamensis fossil sites, formation sites and palaeoenvironment sites mentioned in the text were plotted using curated locality data and georeferenced coordinates. The hominin fossil localities plotted in this figure are listed in Supplementary Table S1; selected formation and palaeoenvironmental reference localities are included for geographic context and are cited in the manuscript.*

Drapeau et al. [107] reported 250 fossil specimens from Mursi, yet unexpectedly, no primates and, in particular, no hominins were identified. Given the rarity of hominins in systematic Omo-Turkana assemblages, non-recovery at a single site is not conclusive, but the result remains noteworthy. In contrast, *Australopithecus anamensis*, the oldest known hominin in the basin, is present at Kanapoi (4.2 to 4.1 Ma) and Allia Bay (3.97 Ma) (Figure 8), and the palaeoenvironments of those sites are well understood [110-113], providing useful environmental reference points against which proposed dispersal corridors can be assessed.

To evaluate the contrast between the recovery of *Australopithecus anamensis* at Kanapoi and Allia Bay and its non-recovery at Mursi, Dumouchel [114] conducted a comparative analysis of these three fossil localities. The prevailing explanation is that *A. anamensis* was more common in relatively open, seasonally dry habitats, and absent in more humid or closed settings. Beasley [115], however, offered an alternative interpretation, suggesting the non-recovery of hominins at Mursi may reflect sampling limitations.

Dumouchel and Drapeau [116] later extended this work through taphonomic analyses of the fossil fauna from the Mursi Formation and Member A of the Shungura Formation. They concluded that these two depositional settings are remarkably similar (Figure 8). Yet despite this, no hominins have been recovered from the Mursi Formation. The chronological ranges are also broadly compatible; the Mursi Formation spans 4.0 to 4.5 Ma and underlies the Shungura Formation (3.59-3.33 Ma), with Dumouchel and Drapeau concluding that fossils found within the Mursi Formation are indeed contemporaneous with those found in Member A of the Shungura Formation.

Taken together, these observations suggest that the non-recovery of hominins at Mursi warrants attention, although it is not sufficient on its own to demonstrate a genuine limit to southward dispersal. In the context of the present study, Mursi is treated as an informative negative case, consistent with, but not decisive for, a scenario in which southward landscape permeability increased as the Main Ethiopian Rift developed into a more effective dispersal corridor by ca. 4.2 Ma. Sampling, preservation, and exposure biases remain alternative explanations. Table 2 places this pattern in broader regional context by summarising reported occurrences of fossil apes and early hominins across Ethiopia, Kenya, and Tanzania.

APE AND HOMININ SPECIES	AGE (MILLION YEARS AGO)	ETHIOPIA	KENYA	TANZANIA
HOMO SAPIENS (EARLY)	>160 ka	Omo Kibish, Herto (Middle Awash)	Widespread	Widespread
HOMO ERECTUS / H. ERGASTER	1.8 - 0.8 Ma	Melka Kunture, Konso	Widespread	Widespread
HOMO HABILIS (FRAGMENTARY)	2.4 - 1.4 Ma	Gona and Omo (tentative)	Yes - Koobi Fora	Yes, Olduvai Gorge
AUSTRALOPITHECUS GARHI	2.5 Ma	Bouri, Middle Awash	Not Found	Not Found
AUSTRALOPITHECUS DEYIREMEDA	3.5 - 3.3 Ma	Woranso-Mille	Not Found	Not Found
AUSTRALOPITHECUS AFARENSIS	3.9 - 3.0 Ma	Hadar, Dikika	Yes	Yes
AUSTRALOPITHECUS ANAMENSIS	4.2 - 3.9 Ma	Asa Issie, Middle Awash	Kanapoi	Not Found
ARDIPITHECUS RAMIDUS	4.4 Ma	Aramis, Afar Depression	Not Found	Not Found
ARDIPITHECUS KADABBA	5.8 - 5.2 Ma	Middle Awash	Not Found	Not Found
CHORORAPITHECUS ABYSSINICUS	~8 Ma	Chorora Formation	Not Found	Not Found
SAMBURUPITHECUS KIPTALAMI	9.5 Ma	Not Found	Samburu Hills	Not Found
KENYAPITHECUS WICKERI	14 Ma	Not Found	Fort Ternan	Not Found
NACHOLAPITHECUS KERIOI	15 Ma	Not Found	Nachola (Northern Kenya)	Not Found
EQUATORIUS AFRICANUS	15.5 - 15 Ma	Not Found	Cheboit and Tugen Hills	Not Found
AFROPITHECUS TURKANENSIS	17 - 16 Ma	Not Found	Kalodirr (Lake Turkana Basin)	Not Found
TURKANAPITHECUS KALAKOLENSIS	17 - 16 Ma	Not Found	Kalodirr (Lake Turkana Basin)	Not Found
PROCONSUL MAJOR	18 Ma	Not Found	Mfangano Island	Not Found
PROCONSUL HESELONI	18 - 17 Ma	Not Found	Koru, Songhor	Not Found
NYANZAPITHECUS VANCOUVERINGORUM	18 - 17 Ma	Not Found	Songhor	Not Found
NYANZAPITHECUS PICKFORDI	18 - 17 Ma	Not Found	Songhor	Not Found
PROCONSUL NYANZAE	19 - 18 Ma	Not Found	Songhor	Not Found
PROCONSUL AFRICANUS	20 - 18 Ma	Not Found	Rusinga Island	Not Found
RUKWAPITHECUS FLEAGLEI	~25 Ma	Not Found	Not Found	Rukwa Rift Basin
NSUNGWEPITHECUS GUNNELLI	~25 Ma	Not Found	Not Found	Rukwa Rift Basin

Table 2. Distribution of selected Miocene ape and early hominin fossils in Ethiopia, Kenya, and Tanzania. Kenya and Tanzania preserve numerous Miocene ape species but no securely dated, uncontroversial bipedal hominin fossils are currently known older than ca. 4.2 Ma. In contrast, Ethiopia, particularly the Afar region, shows a sequence from facultative to obligate bipedality.

3.3 Omo-Turkana Basin and southward landscape connectivity

Between 5 Ma and 3 Ma, the Turkana, Omo, and Chew Bahir rifts entered their main phase of subsidence and sedimentation in the Omo-Turkana Basin [103, 106, 117]. This rifting and the progressive increase in southward connectivity during this interval likely shifted the distribution of freshwater-linked mosaic habitats southward, reduced regional isolation, and increased landscape permeability within the basin. By the Pliocene, the Kulal, Marsabit, Nyiro, and Ndoto mountains formed a high-node chain, enhancing high-relief connectivity from the Ethiopian Plateau margin of the Central Main Ethiopian Rift into the northern Kenya rift-shoulder massifs [103, 105, 106].

Between 5 Ma and 4 Ma, the Turkana Basin was a dynamic environment that alternated between fluvial, deltaic, and lacustrine settings due to shifting flows of the Omo, Turkwell, and Kerio rivers. At 4.5 Ma, these ancient rivers created the so-called Turkana River in the Apak Plain, which flowed into the Indian Ocean in the southeast [106, 117]. The Omo-Turkana basin filled with palaeo-lake Lonyumun about 4.14 Ma, pushing trees and grasslands to the basin's borders [106, 110, 112, 117]. As Figure 9 shows, the mapped relationship between reconstructed rift structures and early hominin localities supports a route along the escarpment margin extending southward from the MER, which may have enabled movement towards the early hominin localities of Fejej, Allia Bay, and Kanapoi, together with the more debated Chemeron Formation locality at Tabarin. In the framework proposed here, such movement is envisaged as a series of short transfers between adjacent high nodes on the rift shoulder, using tree cover, escarpment relief, ravines, and riparian strips, rather than as a continuous basin-floor traverse.

Comparative studies of small mammals show southward dispersal from Ethiopia to Kenya in the late Pliocene to early Pleistocene (3–2 Ma) [118-120]. While those authors emphasise basin humidification, the spatial pattern is also consistent with a stepwise, high-relief corridor linking the rift-shoulder massifs east of Lake Turkana, without requiring basin-wide humidification or simultaneous dispersal across all taxa.

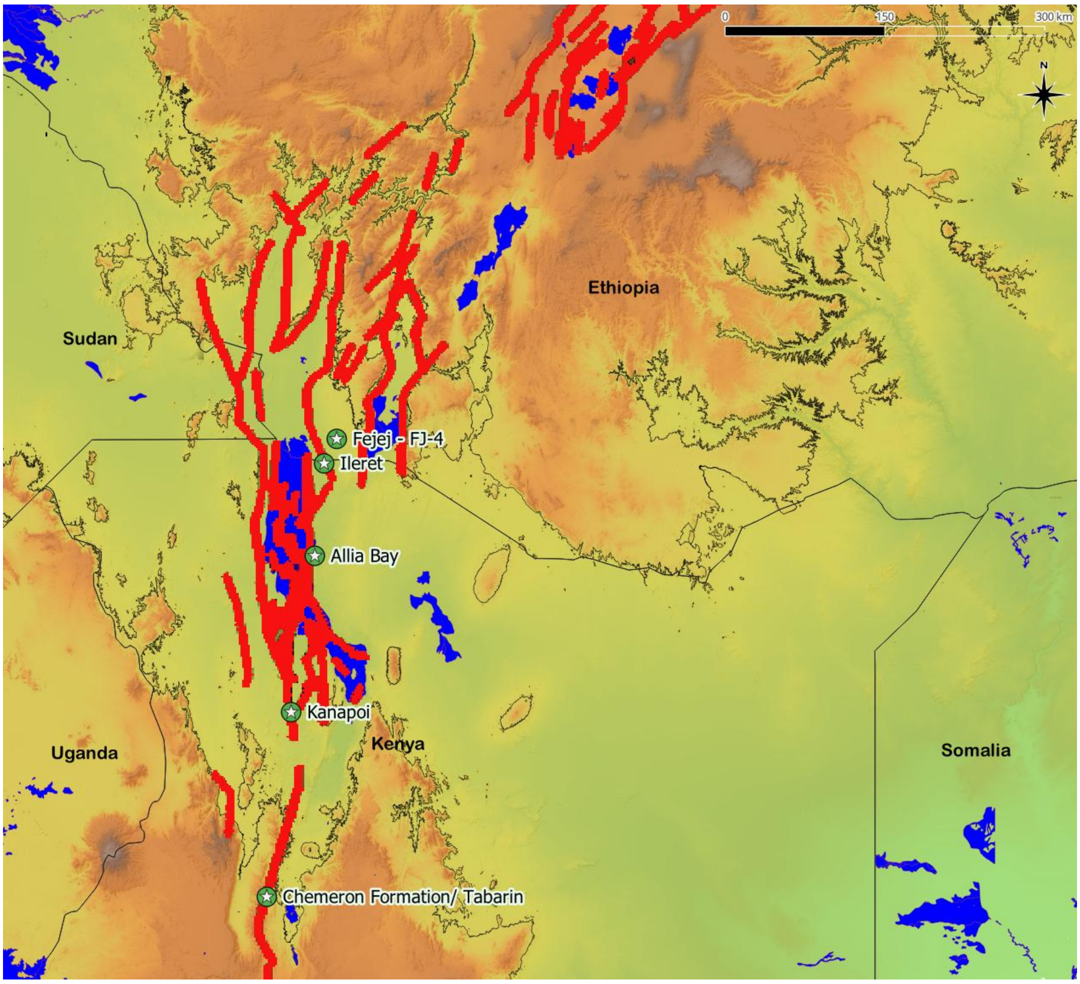

Figure 9. *Proximity of early hominin localities to rift structure. QGIS-generated map of the Turkana Basin based on present-day topography, onto which georeferenced published rift-structure data for the Omo-Turkana area at 5 Ma [103] have been superimposed. Although the basin underwent repeated lacustrine and fluvial reorganisation during this interval, and modern Lake Turkana did not yet exist, the map is intended to show the approximate spatial relationship between early hominin localities and the rift framework reconstructed for that time. Fejej, Allia Bay, and Kanapoi, together with the more debated Chemeron Formation locality at Tabarin, all lie close to major reconstructed rift margins.*

While a few more southerly sites have yielded fragmentary remains that some have interpreted as early hominins, most notably the Lothagam mandible (KNM-LT 329) and the Tabarin mandible (KNM-TH 13150), these specimens remain taxonomically uncertain, as do their dates [121]. They are therefore treated here as possible, but unconfirmed, early hominin occurrences that do not overturn the broader pattern of secure bipedal hominin fossils appearing outside Afar only after about 4.2 Ma.

4. DISCUSSION

4.1 Tectonics, topography, and the early evolution of bipedalism

The evolution of habitual bipedalism has long been framed primarily in relation to climatic drying and the spread of more open habitats. That framing is incomplete if it does not also consider terrain, refuge structure, and predation risk. For early hominins living within African ecosystems containing numerous predators, the transition to more regular upright locomotion would have depended not only on vegetation change, but also on the availability of protective topography and safe movement routes. Thorpe et al. [122] suggest that some degree of facultative bipedalism is relatively common among primates and may arise quite naturally under certain behavioural and ecological conditions, and the fossil record is broadly consistent with this view. Other ape lineages also evolved bipedal behaviours in different parts of the world, indicating that upright locomotion need not be interpreted solely as a response to open savannah conditions.

What tectonic and topographic structure adds to this discussion is a three-dimensional landscape framework. Rifted and uplifted terrains create cliffs, escarpments, ravines, wetlands, springs, and other forms of defensible relief that can reduce exposure to predators, structure habitat continuity, and channel movement between adjacent habitats [27, 28, 81]. These factors are rarely explicit in climate-led accounts of early bipedalism, yet they are directly relevant to how primates move through landscapes, where they sleep, how they avoid predators, and how local populations remain connected or isolated over time [27, 28, 81]. This perspective also overlaps partly with complex topography models, in which rugged relief and climbing or scrambling terrain are treated as important components of early hominin locomotor evolution [123, 124].

The Miocene ape *Oreopithecus* represents one such case, having evolved terrestrial bipedality in the swampy, forested islands of the Tusco-Sardinian region, likely facilitated by an absence of natural predators [6, 125]. This Late Miocene great ape inhabited Tuscany and Sardinia at a time when those areas were isolated from the European mainland [126-128] forming the distinctive faunal setting known as the Tusco-Sardinian palaeobioprovince. *Oreopithecus* exhibits a range of anatomical features that successive authors have described as unique or even bizarre, likely shaped by evolution under insular conditions [129]. Around 6.7 Ma, climate change and renewed connection to the mainland ended this insular phase. The influx of new fauna, including predators, likely contributed to the extinction of *Oreopithecus* [130].

Various theories have been proposed over recent decades to explain a direct link between human and mammalian evolution and climate/aridity, such as the pulsed turnover hypothesis

[19], aridity hypothesis [20, 21], variability selection hypothesis [131], and the pulsed climate variability hypothesis [132]. However, these ideas have been increasingly called into question. McKee [133] argues that hominin bipedality predates the much-heralded climatic changes in the various climate theories, so other factors must also have contributed to this major hominin evolutionary transition. He explains the process of hominin bipedalism as being autocatalytic, driven by self-generating feedback loops where one evolutionary step is a sufficient catalyst for the next, irrespective of changes in the external environment. Maxwell et al. [11] similarly conclude that any apparent links between early hominin diversity and indications of climate instability are likely caused by differences in rock exposure and collection effort.

These critiques are consistent with the view developed here, that aridity and climate variability remain relevant, but do not explicitly address refuge structure, predator buffering, and landscape continuity, all of which may have supported the persistence of early upright behaviours. In this perspective, tectonic and topographic isolation may have been a major, underappreciated component of the context in which early bipedalism evolved, with later increases in connectivity acting as filters on the anatomical, locomotor, and behavioural traits that had accumulated or persisted within refugial settings.

4.2 Afar as a refugial landscape

Taken together, our tectonic and geomorphological reconstruction suggests that the Afar region evolved from an initially open, connected landscape into a tectonically isolated depression. These rifted landscapes likely restricted faunal movement and regional connectivity, and the evolutionary consequences of this are consistent with the high numbers of new mammal species identified in the Miocene Middle Awash deposits [134], as well as high levels of endemism today in rodents and other mammals [135-137], reptiles and fish [88, 138], and plant species [e.g., 139, 140]. This regional structure is consistent with recent palaeobiotic work showing marked differences among East African Rift mammal communities during the late Miocene and early Pliocene, before broader faunal homogenisation became clearer after ca. 3 Ma [141].

A central argument of this paper is that Afar acted as a long-lived refugium during a critical phase of early hominin evolution. Tectonic structure and rugged relief likely limited regional connectivity, shaping persistence and local divergence over time. Rift-margin cliffs, wetlands, and variable drainage may have created defensible terrain and reliable water, allowing early hominins to reduce predation risk while exploiting varied resources. Research in the Plio-Pleistocene Baza Basin of southern Spain shows that tectonic and hydrothermal processes created persistent wetland microrefugia that supported diverse mammal communities [142]. Comparable mechanisms may have operated in Afar, producing localized ecological buffers that helped early hominins manage predation risk and exploit varied niches.

In this refugial scenario, landscape structure is treated as a major influence on early bipedal evolution. The relative isolation of Afar may also have altered the balance between gene flow, local selection, and drift. In small or semi-isolated populations, novel traits, including early forms of bipedality, may have become established through a combination of reduced gene flow, local selection, and drift, before being subjected to harsher filtering in more competitive or open environments.

The unique nature of the Afar region has long been recognized, and some authors have referred to it as a refugium despite its vast area, around 100,000 square kilometres, and its constantly changing geomorphology over the past 30 million years. Here, however, Afar is not envisaged as a single uniform refugium. Rather, the concepts of refugia-within-refugia [see 143] and microrefugia [144] help explain how endemism and speciation could have operated at much smaller and more localized scales within a larger tectonically unstable region. We suggest that the ongoing volcanism and rifting repeatedly shifted these localized refugial settings from one valley to the next, enabling hominins to track these changes, possibly via cliff conduits and other topographic corridors. This interpretation partly overlaps with the complex topography hypothesis [123, 124], in which hominins are proposed to have developed substantial reliance on bipedalism through movement across steep hillslopes and rock faces generated by tectonic and rifting processes. The Hadar and Busidima Formations tuffs suggest highly localized “basin-scale geological processes” in Afar [145], and this is consistent with the close proximity of Dikika, Gona, Hadar, and Ledi-Geraru, where refugial conditions may have varied across very short distances. Although these sites now lie on uplifted ground away from active volcanism, they were once located nearer the rift-valley floor [81], providing a confined setting for hominin persistence and local differentiation.

During the *Ardipithecus* interval, increasing isolation of Afar, together with wooded habitats and relatively low observed carnivore diversity, is consistent with restricted-connectivity conditions in which early bipedal behaviours may have persisted. In this interpretation, Afar differed from more open and connected systems in predation exposure, habitat continuity, and access to defensible terrain.

4.3 Opening of the MER and the timing of southward dispersal

If Afar functioned as a long-term refugial setting, the next question is when and how that isolation weakened sufficiently to permit southward dispersal. The evidence reviewed here indicates that late reorganisation of the Central Main Ethiopian Rift was the most plausible tectonic development increasing southward connectivity and establishing a more throughgoing inland corridor between Afar and the Turkana Basin. The timing of this transition remains uncertain, but ca. 4.2 Ma is treated here as a provisional working horizon, subject to revision as new chronology and fossil discoveries become available.

Taken together, the observations from the Mursi Formation indicate that the non-recovery of hominins there warrants attention, although it is not sufficient on its own to demonstrate a genuine limit to southward dispersal. In the context of the present study, the formation is best treated as an informative but non-decisive constraint within a broader pattern that also includes increasing southward landscape permeability as the Main Ethiopian Rift developed into a more effective dispersal corridor by ca. 4.2 Ma.

As the East African Rift opened southward, the Afar system became linked to more open and competitive landscapes farther south. Joordens et al. [146] have highlighted the possible importance of a coastal refugium in helping explain movements southwards, but the emphasis here is on inland dispersal routes via the MER.

Once hominins dispersed from the MER and into southern Ethiopia and Kenya, they likely encountered different selective pressures. In more open landscapes, exposure to predation and competition may have increased, and natural selection would have favoured individuals better able to move efficiently on the ground while managing predation risk through vigilance, grouping behaviour, and access to protective terrain. Within this framework, increased connectivity may have acted as a selective filter, favouring some traits that had persisted in Afar while eliminating others. The diversification of the australopithecines following the opening of this gateway to the south may therefore reflect increased evolutionary pressures, with only some of the anatomical, locomotor, and behavioural traits that accumulated or persisted under earlier restricted-connectivity conditions persisting in the newly connected system.

4.4 Uncertainty, sampling, and testable expectations

The interpretation proposed here remains contingent on future geological, chronological, and palaeontological revision. In particular, the proposed southward dispersal horizon near ca. 4.2 Ma depends on current understanding of Central MER development and the existing fossil record in the Omo-Turkana region. Within that uncertainty, the refugial connectivity-threshold scenario outlined here implies a series of geographic and chronological expectations that can be evaluated as fossil sampling improves, chronologies are refined, and independent geological indicators are compared across the same intervals. These expectations, alternative explanations, and potential revision triggers are summarised in Table 3.

Table 3. Testable expectations of the refugial-connectivity model.

Model expectation	Supporting pattern	Alternative explanation	What would weaken the model
Early secure hominin records should cluster in Afar/restricted landscapes	Ardipithecus and early Australopithecus records concentrated in Afar	Sampling and exposure bias	Secure older non-Afar records in non-rift or non-refugial settings
Southward records should appear after increased MER permeability	Kanapoi, Allia Bay, Fejej pattern after ca. 4.2 Ma	Earlier unsampled dispersal	Secure earlier southward records
Mursi should be treated as a weak negative constraint	No hominins in reported assemblage	Sampling/preservation bias	Secure hominins from Mursi-aged deposits
Faunal provincialism may persist despite limited corridor permeability	Rowan-style provincialism compatible with uneven dispersal	Observed pattern reflects sampling or taxon-specific ecology rather than permeability change	Evidence of no meaningful Afar isolation or no MER-linked dispersal relevance

One expectation is that early hominin occurrences outside Afar should be biased towards rift margins, faulted uplands, and incised terrain that provided persistent refuge structure and route continuity, rather than being evenly distributed across basin interiors. A second expectation is that dispersal should appear broadly stepwise geographically and chronologically, with the earliest signals emerging first along the Main Ethiopian Rift and adjacent rift-linked corridors before appearing farther south. If a connectivity threshold was crossed near ca. 4.2 Ma, then independent geological and landscape evidence should also indicate that movement became easier during the same interval, including better connected drainage systems and passable links across previously discontinuous rift terrain. Because the mechanism proposed here is landscape permeability rather than a hominin-specific behavioural event, comparable shifts should also be detectable in selected non-hominin taxa sensitive to terrain structure and stepwise habitat continuity across the same corridor.

The Mursi Formation remains particularly important in this regard. If non-recovery of hominins persists across multiple well-sampled Mursi-aged deposits, this would strengthen the interpretation that southward dispersal remained limited during part of that interval. If, however, future work recovers secure hominins from Mursi-aged deposits, this would not invalidate the broader model, but it would suggest that increased landscape permeability, and possibly dispersal beyond Afar, began earlier than the current working horizon of ca. 4.2 Ma, or that the present pattern partly reflects sampling and preservation biases. Table 2, introduced above, provides the wider regional context for this expectation.

The model would also require revision if well-dated, unambiguous bipedal hominins were recovered substantially earlier than the proposed threshold south of the MER, particularly in settings not aligned with rift-margin connectivity. Likewise, revised dating of MER tectonic development, or stronger evidence for alternative dispersal routes, would require reassessment of the timing and route of first dispersal. In practical terms, the present model suggests that future survey and excavation should extend beyond the major lake-basin depocentres to include rift-shoulder deposits, palaeosols, marginal fluvial systems, and former spring-fed settings, which may preserve earlier or more spatially structured signals of dispersal.

5. CONCLUSION

This paper argues that early bipedal traits may have persisted and diversified within a restricted-connectivity refugial landscape in Afar before later southward dispersal became possible through increasing permeability along the Main Ethiopian Rift. The current fossil and palaeoenvironmental record is consistent with bipedal behaviours occurring in a range of settings rather than in one single habitat type. What is emphasized here, however, is not simply the occurrence of bipedal behaviour, but the possibility that tectonically structured, cliff- and rift-dominated landscapes provided the refuge, continuity, and selective buffering needed for bipedality to persist beyond a merely facultative condition. Ape bipedal behaviours are not uniquely African, and *Oreopithecus bambolii* remains a useful insular comparison [125], but the Afar case is distinct in linking long-term tectonic isolation to the persistence, consolidation, and later dispersal of early bipedal traits.

In this paper a refugial scenario for bipedalism is proposed that places greater emphasis on tectonic isolation and geomorphological change as major structuring forces, while recognising climate variability as an interacting factor in hominin evolution. This scenario is complementary to, rather than in opposition to, existing climate-based frameworks [22, 91, 132, 147-149]. Ethiopia is central to this argument because it uniquely preserves, within a single rift system, evidence relevant to all three shorthand stages discussed here, facultative, habitual, and obligate bipedalism [23]. Within this region, the opening of the Main Ethiopian Rift (MER), initiated ca. 5 Ma, reorganised landscapes and dispersal pathways. This landscape transformation may have increased corridor permeability between Afar and the Turkana Basin. In the current record, securely dated bipedal hominins are present in Afar by ca. 5 Ma, while comparable evidence in the Turkana Basin becomes secure after ca. 4.2 Ma [99-102]. Taken together, the present evidence is consistent with the development of a southward corridor along the MER during the late Miocene and early Pliocene, with dispersal into the Turkana Basin by ca. 4.2 Ma.

Previous studies have highlighted the important contrasts in the role of the African regions of eastern versus southern Africa, where eastern Africa appears to be an important centre of speciation and endemism, while southern Africa preserved this biodiversity [70]. The results presented here suggest that regions within East Africa may also have played distinct evolutionary roles.

More broadly, these findings suggest that tectonic activity, landform evolution, and climate interacted to create the environmental conditions under which early bipedalism could emerge, persist, and later disperse. GIS-assisted mapping of successive tectonic stages provides a source-based spatial framework for testing how rift structures, uplift, and basin isolation constrained movement and dispersal. Rather than moving randomly across open landscapes, early hominins may have followed terrain-structured routes shaped by cliffs, valleys, and refugial topography. Building on this framework, Least Cost Path modelling could incorporate these preferences and provide a predictive tool for identifying dispersal routes that directly link tectonic and landscape changes with evolutionary dynamics. This would allow testing of whether early hominin movement is better explained by rift-shoulder corridors and escarpment-linked, stepwise transfers between refugial nodes than by broad basin-floor dispersal. Such modelling would offer a practical next step for testing the spatial predictions generated by the present refugial scenario.

Rather than dismissing climate-based or anatomical models, this refugial scenario provides a more explicit geological context for understanding how and why early bipedality emerged where it did. By emphasizing the evolutionary impact of tectonic isolation, it helps address fossil distribution patterns that remain challenging for existing frameworks to explain. Geomorphological complexity may have enabled repeated cycles of isolation and reconnection that shaped hominin adaptation in ways under-recognised in current models. Although the fossil record remains patchy, the scenario presented here offers a geologically informed framework that can be refined and tested as new fossil discoveries and geomorphic reconstructions become available. If supported, it may have broader implications for understanding how topographic refugia such as Afar, and corridors such as the Main Ethiopian Rift, functioned as settings for evolutionary innovation.

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Data Availability Statement: This study provides a compiled analytical locality dataset derived from published fossil, geological, palaeoenvironmental, and coordinate sources. The hominin fossil locality records used to generate the fossil point layer in the relevant figures are provided as Supplementary Table S1. No new fossil specimens, primary geological measurements, or quantitative route-modelling outputs were generated for this study. The spatial synthesis and figures were produced from published geological, tectonic, palaeoenvironmental, and fossil-locality sources cited in the manuscript, together with a restricted analytical extract from a broader private locality database compiled during the wider research project. This extract includes a source-checked set of verified hominin locality records, with locality names, ages, taxonomic assignments, formation contexts, geographic coordinates, coordinate precision, taxonomic confidence, and landscape and rift context harmonised against the cited literature where possible. These verified locality records were used to plot the hominin sites shown in the relevant figures. The master database remains a private research asset and is not itself the dataset analysed in this paper. The evidence supporting the interpretations is contained within the article, its figures, Supplementary Table S1, and the cited literature.

Supplementary Table S1 is a restricted analytical extract from a broader author-compiled georeferenced database. The full working database includes additional later hominin, archaeological, and comparative records outside the scope of this paper and is not released here.

REFERENCES

1. Moucha, R. and A.M. Forte, *Changes in African topography driven by mantle convection.* Nature Geoscience, 2011. **4**(10): p. 707–712.
2. Retallack, G.J., *Cenozoic expansion of grasslands and climatic cooling.* The Journal of Geology, 2001. **109**(4): p. 407–426.
3. Cote, S., et al., *Evidence for rapid faunal change in the early Miocene of East Africa based on revised biostratigraphic and radiometric dating of Bukwa, Uganda.* Journal of Human Evolution, 2018. **116**: p. 95–107.
4. Couvreur, T.L.P., et al., *Tectonics, climate and the diversification of the tropical African terrestrial flora and fauna.* Biological Reviews, 2021. **96**(1): p. 16–51.
5. Stevens, N.J., et al., *Palaeontological evidence for an Oligocene divergence between Old World monkeys and apes.* Nature, 2013. **497**(7451): p. 611–614.
6. Hammond, A.S., et al., *Insights into the lower torso in late Miocene hominoid Oreopithecus bambolii.* Proceedings of the National Academy of Sciences, 2020. **117**(1): p. 278–284.
7. Reynolds, S.C. and R. Bobe, *African Paleoecology and Human Evolution*. 2022: Cambridge University Press.
8. Urciuoli, A. and D.M. Alba, *Systematics of Miocene apes: State of the art of a neverending controversy.* Journal of Human Evolution, 2023. **175**: p. 103309.
9. Behrensmeyer, A., S. Kidwell, and R. Gastaldo, *Taphonomy and paleobiology.* Paleobiology, 2000. **26**: p. 103–147.
10. Faith, J.T., et al., *Rethinking the ecological drivers of hominin evolution.* Trends in Ecology & Evolution, 2021. **36**(9): p. 797–807.
11. Maxwell, S.J., et al., *Sporadic sampling, not climatic forcing, drives observed early hominin diversity.* Proceedings of the National Academy of Sciences, 2018. **115**(19): p. 4891–4896.
12. Richmond, B.G., D.R. Begun, and D.S. Strait, *Origin of human bipedalism: the knuckle-walking hypothesis revisited.* American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists, 2001. **116**(S33): p. 70–105.
13. Pickford, M., et al., *Bipedalism in Orrorin tugenensis revealed by its femora.* Comptes Rendus Palevol, 2002. **1**(4): p. 191–203.
14. Lovejoy, C.O., et al., *The pelvis and femur of Ardipithecus ramidus: the emergence of upright walking.* Science, 2009. **326**(5949): p. 71–71e6.
15. Haile-Selassie, Y., et al., *A new hominin foot from Ethiopia shows multiple Pliocene bipedal adaptations.* Nature, 2012. **483**(7391): p. 565–569.
16. Lovejoy, C.O. and M.A. McCollum, *Spinopelvic pathways to bipedality: why no hominids ever relied on a bent-hip–bent-knee gait.* Philosophical Transactions of the Royal Society B: Biological Sciences, 2010. **365**(1556): p. 3289–3299.
17. Daver, G., et al., *Postcranial evidence of late Miocene hominin bipedalism in Chad.* Nature, 2022. **609**(7925): p. 94–100.
18. Lawrence, A.B., A.S. Hammond, and C.V. Ward, *Acetabular orientation, pelvic shape, and the evolution of hominin bipedality.* Journal of Human Evolution, 2025. **200**: p. 103633.
19. Vrba, E.S., *Turnover-pulses, the Red Queen, and related topics.* American Journal of Science, 1993. **293**(A): p. 418.
20. deMenocal, P.B., *Plio-pleistocene African climate.* Science, 1995. **270**(5233): p. 53–59.
21. deMenocal, P.B., *African climate change and faunal evolution during the Pliocene–Pleistocene.* Earth and Planetary Science Letters, 2004. **220**(1–2): p. 3–24.
22. Behrensmeyer, A.K., *Climate change and human evolution.* Science, 2006. **311**(5760): p. 476–478.
23. Stamos, P.A. and Z. Alemseged, *Hominin locomotion and evolution in the Late Miocene to Late Pliocene.* Journal of Human Evolution, 2023. **178**: p. 103332.
24. Villmoare, B., et al., *New discoveries of Australopithecus and Homo from Ledi-Geraru, Ethiopia.* Nature, 2025.
25. Hunt, K.D., *The postural feeding hypothesis: an ecological model for the evolution of bipedalism.* South African Journal of Science, 1996. **92**(2): p. 77–90.

26. Senut, B., et al., *Palaeoenvironments and the origin of hominid bipedalism.* Historical Biology, 2018. **30**(1-2): p. 284–296.
27. Reynolds, S.C., G.N. Bailey, and G.C. King, *Landscapes and their relation to hominin habitats: case studies from Australopithecus sites in eastern and southern Africa.* Journal of Human Evolution, 2011. **60**(3): p. 281–298.
28. Bailey, G.N., S.C. Reynolds, and G.C. King, *Landscapes of human evolution: models and methods of tectonic geomorphology and the reconstruction of hominin landscapes.* Journal of Human Evolution, 2011. **60**(3): p. 257–280.
29. Sepulchre, P., et al., *Tectonic uplift and Eastern Africa aridification.* Science, 2006. **313**(5792): p. 1419–1423.
30. Alemseged, Z., *Reappraising the palaeobiology of Australopithecus.* Nature, 2023. **617**(7959): p. 45–54.
31. Johanson, D.C., T.D. White, and Y. Coppens, *A new species of the genus Australopithecus (Primates: Hominidae) from the Pliocene of eastern Africa.* Kirtlandia, 1978. **28**: p. 1–14.
32. White, T.D., G. Suwa, and B. Asfaw, *Australopithecus ramidus, a new species of early hominid from Aramis, Ethiopia.* Nature, 1994. **371**(6495): p. 306–312.
33. White, T.D., G. Suwa, and B. Asfaw, *Corrigendum: Australopithecus ramidus, a new species of early hominid from Aramis, Ethiopia.* Nature, 1995. **375**(6526): p. 88.
34. Villmoare, B., et al., *Early Homo at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia.* Science, 2015. **347**(6228): p. 1352–1355.
35. Arambourg, C. and Y. Coppens, *Sur la découverte, dans le Pléistocène inférieur de la vallée de l’Omo (Éthiopie), d’une mandibule d’australopithécien.* Comptes Rendus des seances de l'Academie des Sciences, 1968. **265**: p. 589–590.
36. Asefa, M., et al., *Ethiopian vegetation types, climate and topography.* Plant Diversity, 2020. **42**(4): p. 302–311.
37. Demissew, S., I. Friis, and O. Weber, *Diversity and endemism of the flora of Ethiopia and Eritrea: state of knowledge and future perspectives.* Rendiconti Lincei. Scienze Fisiche e Naturali, 2021. **32**(4): p. 675–697.
38. Sani, F., et al., *Evolution of the northern tip of Afar triangle: Inferences from the Quaternary succession of the Dandiero — Massawa area (Eritrea).* Tectonophysics, 2017. **717**: p. 339–357.
39. Slatkin, M., *Gene flow and the geographic structure of natural populations.* Science, 1987. **236**(4803): p. 787–792.
40. Mayr, E., *Animal Species and Evolution*. 1963, Cambridge, MA: Harvard University Press.
41. Hewitt, G., *The genetic legacy of the Quaternary ice ages.* Nature, 2000. **405**(6789): p. 907–913.
42. Seiffert, E.R., *Early primate evolution in Afro-Arabia.* Evolutionary Anthropology: Issues, News, and Reviews, 2012. **21**(6): p. 239–253.
43. Gheerbrant, E. and J.-C. Rage, *Paleobiogeography of Africa: How distinct from Gondwana and Laurasia?* Palaeogeography, Palaeoclimatology, Palaeoecology, 2006. **241**(2): p. 224–246.
44. Rage, J.-C. and E. Gheerbrant, *Island Africa and Vertebrate Evolution: A Review of Data and Working Hypotheses*, in *Biological Consequences of Plate Tectonics*. 2020, Springer International Publishing. p. 251–264.
45. Sen, S., *Dispersal of African mammals in Eurasia during the Cenozoic: ways and whys.* Geobios, 2013. **46**(1-2): p. 159–172.
46. Stanhope, M.J., et al., *Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals.* Proceedings of the National Academy of Sciences, 1998. **95**(17): p. 9967–9972.
47. Meredith, R.W., et al., *Impacts of the Cretaceous Terrestrial Revolution and KPg extinction on mammal diversification.* Science, 2011. **334**(6055): p. 521–524.
48. McQuarrie, N., et al., *Cenozoic evolution of Neotethys and implications for the causes of plate motions.* Geophysical Research Letters, 2003. **30**(20).
49. Mattingly, S., *New Eurasian Immigrants in the Late Paleogene of Africa, and the Great Old World Biotic Interchange: A Quantitative Analysis of Mammalian Dispersal*. 2022, University of Kansas.

50. Steiper, M.E. and E.R. Seiffert, *Evidence for a convergent slowdown in primate molecular rates and its implications for the timing of early primate evolution.* Proceedings of the National Academy of Sciences, 2012. **109**(16): p. 6006–6011.
51. Rogers, N., *Basaltic magmatism and the geodynamics of the East African Rift System.* Geological Society, London, Special Publications, 2006. **259**(1): p. 77–93.
52. Nyblade, A.A. and S.W. Robinson, *The african superswell.* Geophysical Research Letters, 1994. **21**(9): p. 765–768.
53. Lithgow-Bertelloni, C. and P.G. Silver, *Dynamic topography, plate driving forces and the African superswell.* Nature, 1998. **395**: p. 269.
54. Gani, N.D. and P.C. Neupane, *Understanding transient landscape of the Ethiopian Plateau in relation to mantle dynamics.* Geological Journal, 2018. **53**(1): p. 371–385.
55. Sembroni, A., et al., *Long-term, deep-mantle support of the Ethiopia-Yemen Plateau.* Tectonics, 2016. **35**(2): p. 469–488.
56. Xue, L., et al., *Spatial and temporal variation of tectonic uplift in the southeastern Ethiopian Plateau from morphotectonic analysis.* Geomorphology, 2018. **309**: p. 98–111.
57. Mohr, P. and B. Zanettin, *The Ethiopian Flood Basalt Province*, in *Continental Flood Basalts*, J.D. Macdougall, Editor. 1988, Springer Netherlands: Dordrecht. p. 63–110.
58. Ukstins, I.A., et al., *Matching conjugate volcanic rifted margins: 40Ar/39Ar chrono-stratigraphy of pre- and syn-rift bimodal flood volcanism in Ethiopia and Yemen.* Earth and Planetary Science Letters, 2002. **198**(3): p. 289–306.
59. Seiffert, E.R., et al., *Basal Anthropoids from Egypt and the Antiquity of Africa's Higher Primate Radiation.* Science, 2005. **310**(5746): p. 300–304.
60. Seiffert, E.R., et al., *Additional remains of Wadilemur elegans, a primitive stem galagid from the late Eocene of Egypt.* Proceedings of the National Academy of Sciences, 2005. **102**(32): p. 11396–11401.
61. Murray, A.M., et al., *A freshwater ichthyofauna from the late Eocene Birket Qarun Formation, Fayum, Egypt.* Journal of Vertebrate Paleontology, 2010. **30**(3): p. 665–680.
62. Gentzis, T., et al., *Depositional environment and characteristics of Late Eocene carbonaceous swampy tidal flat facies in the Fayoum Basin, Egypt.* International Journal of Coal Geology, 2018. **200**: p. 45–58.
63. El-Sayed, S., et al., *Oldest Record of African Bagridae and Evidence from Catfishes for a Marine Influence in the Late Eocene Birket Qarun Locality 2 (BQ-2), Fayum Depression, Egypt.* Journal of Vertebrate Paleontology, 2020. **40**(3): p. e1780248.
64. Seiffert, E.R., *Revised age estimates for the later Paleogene mammal faunas of Egypt and Oman.* Proceedings of the National Academy of Sciences, 2006. **103**(13): p. 5000–5005.
65. Olson, S.L. and D.T. Rasmussen, *Paleoenvironment of the earliest hominoids: new evidence from the Oligocene avifauna of Egypt.* Science, 1986. **233**(4769): p. 1202–1204.
66. Murray, A.M., *Late Eocene and early Oligocene teleost and associated ichthyofauna of the Jebel Qatrani Formation, Fayum, Egypt.* Palaeontology, 2004. **47**(3): p. 711–724.
67. Holmes, R.B., et al., *Agamid lizard (Agamidae: Uromastycinae) from the lower Oligocene of Egypt.* Historical Biology, 2010. **22**(1-3): p. 215–223.
68. Kampouridis, P., J. Hartung, and F.J. Augustin, *The Eocene–Oligocene vertebrate assemblages of the Fayum Depression, Egypt*, in *The Phanerozoic Geology and Natural Resources of Egypt*. 2023, Springer. p. 373–405.
69. Vignaud, P., et al., *Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad.* Nature, 2002. **418**(6894): p. 152–155.
70. Reynolds, S.C., *Mammalian body size changes and Plio-Pleistocene environmental shifts: implications for understanding hominin evolution in eastern and southern Africa.* Journal of Human Evolution, 2007. **53**(5): p. 528–548.
71. Schettino, A., C. Macchiavelli, and N.M.A. Rasul, *Plate Motions Around the Red Sea Since the Early Oligocene*, in *Geological Setting, Palaeoenvironment and Archaeology of the Red Sea*. 2019. p. 203–220.
72. Reilinger, R. and S. McClusky, *Nubia–Arabia–Eurasia plate motions and the dynamics of Mediterranean and Middle East tectonics.* Geophysical Journal International, 2011. **186**(3): p. 971–979.

73. Zwaan, F., et al., *A review of tectonic models for the rifted margin of Afar: implications for continental break-up and passive margin formation.* Journal of African Earth Sciences, 2020: p. 103649.
74. Gani, N., M. Gani, and M. Abdelsalam, *Blue Nile incision on the Ethiopian Plateau: Pulsed plateau growth, Pliocene uplift, and hominin evolution.* GSA Today, 2007. **17**(9).
75. Sembroni, A., et al., *Evolution of continental-scale drainage in response to mantle dynamics and surface processes: An example from the Ethiopian Highlands.* Geomorphology, 2016. **261**: p. 12–29.
76. Macgregor, D.S., *The development of the Nile drainage system: integration of onshore and offshore evidence.* Petroleum Geoscience, 2012. **18**(4): p. 417–431.
77. Fielding, L., et al., *The initiation and evolution of the River Nile.* Earth and Planetary Science Letters, 2018. **489**: p. 166–178.
78. Abdelsalam, M.G., *The Young Nile.* Sedimentary Geology, 2021. **421**: p. 105946.
79. Kappelman, J., et al., *Oligocene mammals from Ethiopia and faunal exchange between Afro-Arabia and Eurasia.* Nature, 2003. **426**(6966): p. 549–552.
80. Jacobs, B.F., et al., *Oligocene terrestrial strata of northwestern Ethiopia: a preliminary report on paleoenvironments and paleontology.* Palaeontologia electronica [electronic resource]. Vol. 8, no. 1 (2005): 19 p., 2005.
81. King, G. and G. Bailey, *Tectonics and human evolution.* Antiquity, 2006. **80**(308): p. 265–286.
82. Leakey, M., et al., *Faunal change in the Turkana Basin during the late Oligocene and Miocene.* Evolutionary Anthropology: Issues, News, and Reviews, 2011. **20**(6): p. 238–253.
83. Zwaan, F., et al., *Structural analysis of the Western Afar Margin, East Africa: evidence for multiphase rotational rifting.* Tectonics, 2020. **39**(7): p. e2019TC006043.
84. Redfield, T.F., W.H. Wheeler, and M. Often, *A kinematic model for the development of the Afar Depression and its paleogeographic implications.* Earth and Planetary Science Letters, 2003. **216**(3): p. 383–398.
85. Bosworth, W., P. Huchon, and K. McClay, *The Red Sea and Gulf of Aden basins.* Journal of African Earth Sciences, 2005. **43**(1-3): p. 334–378.
86. Fernandes, C.A., E.J. Rohling, and M. Siddall, *Absence of post-Miocene Red Sea land bridges: biogeographic implications.* Journal of Biogeography, 2006. **33**(6): p. 961–966.
87. Orszag-Sperber, F., et al., *Gypsum salina–coral reef relationships during the Last Interglacial (marine isotopic stage 5e) on the Egyptian Red Sea coast: A Quaternary analogue for Neogene marginal evaporites?* Sedimentary Geology, 2001. **140**(1-2): p. 61–85.
88. Stewart, K.M. and A.M. Murray, *Biogeographic implications of fossil fishes from the Awash River, Ethiopia.* Journal of Vertebrate Paleontology, 2017. **37**(1): p. e1269115.
89. Grossman, A., et al., *First record of Sivameryx (Cetartiodactyla, Anthracotheriidae) from the lower Miocene of Israel highlights the importance of the Levantine Corridor as a dispersal route between Eurasia and Africa.* Journal of Vertebrate Paleontology 2019. **39**(2): p. e1599901.
90. Gilbert, C.C., et al., *Early guenon from the late Miocene Baynunah Formation, Abu Dhabi, with implications for cercopithecoid biogeography and evolution.* Proceedings of the National Academy of Sciences, 2014. **111**(28): p. 10119–10124.
91. Gilbert, C.C. and A. Hill, *Primates from the Baynunah Formation*, in *Sands of Time: Ancient Life in the Late Miocene of Abu Dhabi, United Arab Emirates*. 2022, Springer International Publishing. p. 203–218.
92. Harrison, T., *Apes among the tangled branches of human origins.* Science, 2010. **327**(5965): p. 532–534.
93. White, T.D., et al., *Macrovertebrate paleontology and the Pliocene habitat of Ardipithecus ramidus.* Science, 2009. **326**(5949): p. 87–93.
94. Simpson, S.W., et al., *Late Miocene hominin teeth from the Gona Paleoanthropological Research Project area, Afar, Ethiopia.* Journal of Human Evolution, 2015. **81**: p. 68–82.
95. Cerling, T.E., et al., *Woody cover and hominin environments in the past 6 million years.* Nature, 2011. **476**(7358): p. 51–6.
96. Louchart, A., et al., *Taphonomic, avian, and small-vertebrate indicators of Ardipithecus ramidus habitat.* Science, 2009. **326**(5949): p. 66e1–4.
97. O'Regan, H.J. and S. Reynolds, *An ecological reassessment of the southern African carnivore guild: a case study from Member 4, Sterkfontein, South Africa.* Journal of Human Evolution, 2009. **57**(3): p. 212–222.

98. Haile-Selassie, Y. and G. WoldeGabriel, *Ardipithecus kadabba: late miocene evidence from the Middle Awash, Ethiopia*. 2009, Univ of California Press.
99. Corti, G., et al., *Quaternary volcano-tectonic activity in the Soddo region, western margin of the Southern Main Ethiopian Rift.* Tectonics, 2013. **32**(4): p. 861–879.
100. Abebe, T., M.L. Balestrieri, and G. Bigazzi, *The central Main Ethiopian rift is younger than 8 Ma: Confirmation through apatite fission-track thermochronology.* Terra Nova, 2010. **22**(6): p. 470–476.
101. Bonini, M., et al., *Evolution of the Main Ethiopian Rift in the frame of Afar and Kenya rifts propagation.* Tectonics, 2005. **24**(1).
102. Keir, D., et al., *The origin of along-rift variations in faulting and magmatism in the Ethiopian Rift.* Tectonics, 2015. **34**(3): p. 464–477.
103. Macgregor, D., *History of the development of the East African Rift System: A series of interpreted maps through time.* Journal of African Earth Sciences, 2015. **101**: p. 232–252.
104. Franceschini, Z., et al., *Pulsatory volcanism in the Main Ethiopian Rift and its environmental consequences.* Communications Earth & Environment, 2024. **5**(1): p. 568.
105. Bussmann, R.W., *Islands in the Desert—Forest Vegetation of Kenya'S Smaller Mountains and Highland Areas (Nyiru, Ndoto, Kulal, Marsabit, Loroghi, Ndare, Mukogodo, Porror, Mathews, Gakoe, Imenti, Ngaia, Nyambeni, Loita, Nguruman, Nairobi).* Journal of East African Natural History, 2002. **91**(1): p. 27–79, 53.
106. Feibel, C.S., *A Geological History of the Turkana Basin.* Evolutionary Anthropology: Issues, News, and Reviews, 2011. **20**(6): p. 206–216.
107. Drapeau, M.S., et al., *The Omo Mursi formation: A window into the east African Pliocene.* Journal of Human Evolution, 2014. **75**: p. 64–79.
108. Butzer, K.W. and D. Thurber, *Some late Cenozoic sedimentary formations of the Lower Omo Basin.* Nature, 1969. **222**: p. 1138–1143.
109. Coppens, Y., *Evolution of the hominids and of their environment during the Plio-Pleistocene in the lower Omo Valley, Ethiopia.* Geological Society, London, Special Publications, 1978. **6**(1): p. 499–506.
110. Bobe, R., et al., *The ecology of Australopithecus anamensis in the early Pliocene of Kanapoi, Kenya.* Journal of Human Evolution, 2020: p. 102717.
111. Frost, S.R., et al., *Cercopithecid fossils from Kanapoi, West Turkana, Kenya (2007–2015).* Journal of Human Evolution, 2020: p. 102642.
112. Manthi, F.K., J.M. Plavcan, and C.V. Ward, *Introduction to special issue Kanapoi: Paleobiology of a Pliocene site in Kenya.* Journal of Human Evolution, 2020: p. 102718.
113. Dumouchel, L., et al., *The environments of Australopithecus anamensis at Allia Bay, Kenya: A multiproxy analysis of early Pliocene Bovidae.* Journal of Human Evolution, 2021. **151**: p. 102928.
114. Dumouchel, L., *A multi-proxy analysis of Australopithecus anamensis paleoecology in the Omo-Turkana Basin*. 2018, The George Washington University.
115. Beasley, M.M., *Seasonal precipitation at a 3.97 Ma Australopithecus anamensis site, Allia Bay, Kenya*. 2016, University of California, San Diego.
116. Dumouchel, L. and M. Drapeau, *Taphonomic study of the fossil fauna from the Mursi Formation and Member A of the Shungura Formation, Ethiopia*, in *American Journal of Physical Anthropology*. 2014. p. 110–110.
117. Feibel, C.S. and P. Schwindinger. *Paleogeography of Lake Turkana [online map]*. 2012 [Accessed: January 2025]; Available from: https://education.nationalgeographic.org/resource/paleogeography-lake-turkana/.
118. Šumbera, R., et al., *Ethiopian highlands as a cradle of the African fossorial root-rats (genus Tachyoryctes), the genetic evidence.* Molecular Phylogenetics and Evolution, 2018. **126**: p. 105–115.
119. Lavrenchenko, L.A., et al., *Morphometric and genetic study of Ethiopian Lophuromys flavopunctatus Thomas, 1888 species complex with description of three new 70-chromosomal species (Muridae, Rodentia).* Bull. Inst. R. Sci. Nat. Belg. Biol, 2007. **77**: p. 77–117.
120. Dianat, M., et al., *How to cross the desert if you are small and need mountains? Out-of-Ethiopia dispersal in Afromontane shrews.* Journal of Biogeography, 2024. **51**(2): p. 230–245.
121. Kissel, M. and J. Hawks, *What are the Lothagam and Tabarin Mandibles?* PaleoAnthropology, 2015. **2015**: p. 37–43.

122. Thorpe, S.K.S., J.M. McClymont, and R.H. Crompton, *The arboreal origins of human bipedalism.* Antiquity, 2014. **88**(341): p. 906–914.
123. Winder, I.C., et al., *Evolution and dispersal of the genus Homo: A landscape approach.* Journal of Human Evolution, 2015. **87**: p. 48–65.
124. Winder, I.C., et al., *Complex topography and human evolution: the missing link.* Antiquity, 2013. **87**(336): p. 333–349.
125. Rook, L., et al., *Oreopithecus was a bipedal ape after all: Evidence from the iliac cancellous architecture.* Proceedings of the National Academy of Sciences, 1999. **96**(15): p. 8795–8799.
126. Sartori, R., *Corsica—Sardinia block and the Tyrrhenian Sea*, in *Anatomy of an Orogen: the Apennines and Adjacent Mediterranean Basins*, G.B. Vai and I.P. Martini, Editors. 2001, Springer Netherlands: Dordrecht. p. 367–374.
127. Rook, L., et al., *Il giacimento paleontologico di Fiume Santo. Stato delle ricerche e prospettive a dieci anni dalla scoperta.* Il giacimento paleontologico di Fiume Santo. Stato delle ricerche e prospettive a dieci anni dalla scoperta, 2006: p. 1000–1009.
128. Rook, L., G. Gallai, and D. Torre, *Lands and endemic mammals in the Late Miocene of Italy: constrains for paleogeographic outlines of Tyrrhenian area.* Palaeogeography, Palaeoclimatology, Palaeoecology, 2006. **238**(1-4): p. 263–269.
129. Köhler, M. and S. Moyà-Solà, *Ape-like or hominid-like? The positional behavior of Oreopithecus bambolii reconsidered.* Proceedings of the National Academy of Sciences, 1997. **94**(21): p. 11747–11750.
130. DeMiguel, D. and L. Rook, *Understanding climate's influence on the extinction of Oreopithecus (late Miocene, Tusco-Sardinian paleobioprovince, Italy).* Journal of Human Evolution, 2018. **116**: p. 14–26.
131. Potts, R., *Environmental hypotheses of hominin evolution.* American Journal Of Physical Anthropology, 1998. **107**(S27): p. 93–136.
132. Maslin, M.A., et al., *East African climate pulses and early human evolution.* Quaternary Science Reviews, 2014. **101**: p. 1–17.
133. McKee, J.K., *Correlates and catalysts of hominin evolution in Africa.* Theory in Biosciences, 2017. **136**(3-4): p. 123–140.
134. Vrba, E.S. and Y. Haile-Selassie, *A new antelope, Zephyreduncinus oundagaisus (Reduncini, Artiodactyla, Bovidae), from the late Miocene of the Middle Awash, Afar Rift, Ethiopia.* Journal of Vertebrate Paleontology, 2006. **26**(1): p. 213–218.
135. Yalden, D. and M. Largen, *The endemic mammals of Ethiopia.* Mammal Review, 1992. **22**(3-4): p. 115–150.
136. Tefera, M., *Wildlife in Ethiopia: endemic large mammals.* World Journal of Zoology, 2011. **6**(2): p. 108–116.
137. Bryja, J., et al., *Rodents of the Afar Triangle (Ethiopia): geographical isolation causes high level of endemism.* Biodiversity and Conservation, 2022. **31**(2): p. 629–650.
138. Wagner, P., et al., *Additions to the lizard diversity of the Horn of Africa: Two new species in the Agama spinosa group.* Amphibia-Reptilia, 2013. **34**(3): p. 363–387.
139. Friis, I., et al. *Patterns of plant diversity and endemism in the Horn of Africa*. in *Plant Diversity and Complexity Patterns: Local, Regional, and Global Dimensions: Proceedings of an International Symposium Held at the Royal Danish Academy of Sciences and Letters in Copenhagen, Denmark, 25-28 May, 2003*. 2005. Kgl. Danske Videnskabernes Selskab.
140. Wang, S.W., et al., *Floristic composition and endemism pattern of vascular plants in Ethiopia and Eritrea.* Journal of Systematics and Evolution, 2020. **58**(1): p. 33–42.
141. Rowan, J., et al., *Long-term biotic homogenization in the East African Rift System over the last 6 million years of hominin evolution.* Nature Ecology and Evolution, 2024. **8**(9): p. 1751–1759.
142. García-Aguilar, J.M., et al., *Plio-Pleistocene hydrothermal events of the Baza Basin (Betic Cordillera, SE Spain) and their paleoecological implications.* Journal of Iberian Geology, 2024: p. 1–37.
143. Abellán, P. and J.-C. Svenning, *Refugia within refugia–patterns in endemism and genetic divergence are linked to Late Quaternary climate stability in the Iberian Peninsula.* Biological Journal of the Linnean Society, 2014. **113**(1): p. 13–28.
144. Hylander, K., et al., *Microrefugia: Not for everyone.* Ambio, 2015. **44**(1): p. 60–68.

145. Roman, D., et al., *Composite tephrostratigraphy of the Dikika, Gona, Hadar, and Ledi-Geraru project areas, northern Awash, Ethiopia.* The geology of early humans in the horn of Africa, Special Paper, 2008. **446**: p. 119–134.
146. Joordens, J.C., et al., *Relevance of the eastern African coastal forest for early hominin biogeography.* Journal of Human Evolution, 2019. **131**: p. 176–202.
147. Bobe, R., A.K. Behrensmeyer, and R.E. Chapman, *Faunal change, environmental variability and late Pliocene hominin evolution.* Journal of Human Evolution, 2002. **42**(4): p. 475–497.
148. Bonnefille, R., *Cenozoic vegetation, climate changes and hominid evolution in tropical Africa.* Global and Planetary Change, 2010. **72**(4): p. 390–411.
149. deMenocal, P.B., *Anthropology. Climate and human evolution.* Science, 2011. **331**(6017): p. 540–2.

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